Meddelelser om Grønland.

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The

Structure and Biology

of

Arctic Flowering Plants.

I.

Udgivet paa Carlsbergfondets Bekostning.

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Preface.

The papers collected in the present volume of "Meddelelser om Grønland," under the title "The Structure and Biology of Arctic Flowering plants," have been published by the Commission for the Geographical and Geological Investigations of Greenland, at the suggestion of the two undersigned. The greater part of the material upon which the investigations recorded in the papers in question have been carried out, belongs to the Botanical Museum in Copenhagen, where are preserved the rich collections brought home in the course of the last 35 years by the numerous, almost yearly, Danish expeditions to Greenland. The meagre collections from other Arctic regions and the richer ones from the Scandinavian mountains, from Iceland and the Færöes, belonging to this museum, have also been utilized. Thus the title "Arctic Flowering plants" is in reality too comprehensive, in so far as, no Arctic material, or very little, of plants from other Arctic regions than Greenland, Spitzbergen and Nova Zembla has been available.[1] Sometimes material from Denmark has been used for comparison.

The object of publishing these papers is twofold; firstly to contribute towards a knowledge of the structure and biology of the Arctic flowering plants so far as the material in hand permits of this, and secondly, *inter alia*, by means of numerous illustrations to give a basis for future botanical observations and studies in Arctic countries, made on the spot by the travellers themselves. As a rule so much time is taken up by the journey itself, and the gathering of the material, and the noting of observations of various kinds — often made under difficult and perilous conditions — that scarcely any time is left for more accurate studies on the spot as, for instance, of the biology of the plants and the pollination of the flowers, while even less time is left for investigations of a physiolo-

[1] We speak only of material preserved in alcohol, not of herbarium specimens.

gical nature. It is our hope that biological studies on the spot, which are highly necessary, will be promoted by these papers; just as it is one of the objects of the Danish Arctic Station on Disco to study such biological and physiological problems as require a longer sojourn (summer and winter) at the same place and the help of laboratory instruments.

Moreover, we hope that these papers will also render possible comparisons with the same species from other and quite different regions, e. g. the Temperate or Alpine regions, and also will serve to demonstrate whether differences do occur or do not; after which the question will arise: What reason is there for these differences? In the investigations published in the present volume it has been possible to make such comparisons in only a very few cases, one of the reasons being that the material in hand did not allow of such comparisons; for, usually, the notes regarding the conditions under which the plants were found were not sufficiently exhaustive.

As regards the points which now require to be investigated in Arctic countries, the reader is referred to "Meddelelser om Grönland," vol. XXX, where the instructions given to the botanist of the Amdrup Expedition, Mr. C. Kruuse, have been published. From these we shall here extract some points concerning the Biological questions: —

1. The condition in which plants have passed the winter; whether reserve food-material occurs; whether the flowers are formed the year previous to that in which they open.
2. Spring phenomena.
3. Flowering phenomena: the biology and the shade of colour of the flower; the visits of insects to the flower.
4. Fructification; phenomena connected with the fall of the leaf; dispersal of seed.
5. Observations of the humidity of the air; the temperature of the snow, soil, water and air (in the sunlight and in the shade).
6. The formation of mycorrhiza.
7. Investigations of carbon-assimilation.

For further references see loc. cit.

It may, moreover, be stated that, of the two undersigned, Ostenfeld has revised the determination of the species, while

Warming's part of the work has essentially consisted in giving the authors all such help and instruction as they have wished for.

Some of the biological investigations, especially those concerning the flower-biology of some of the families, Warming published some years ago (1885, 1886) in Danish, in various papers to which reference is made in the lists of literature. In the present volume, as far as is possible, they have been revised and supplemented.

The authors themselves are alone responsible for their own papers.

It is intended that these publications should be continued in vol. XXXVII of Meddelelser om Grønland.

Dr. C. H. Ostenfeld. *Dr. Eug. Warming.*

The

Structure and Biology

of

Arctic Flowering Plants.

1.

Ericineæ (Ericaceæ, Pirolaceæ).

1. Morphology and Biology.

By

Eug. Warming.

1908.

PREFACE.

These notes on the Arctic *Ericineæ* were for the most part published as early as 1885—86 in Botanisk Tidsskrift (København); Det Kgl. Danske Videnskabernes Selskabs Oversigt; and Det Kgl. Svenska Vetenskaps Akademiens Bihang. But as they were written in Danish, they have been but little used by foreign botanists. They have now been collected and published in English in the present (36th) volume of Meddelelser om Grønland, after having been supplemented by additional observations and figures, some of which are old, but have not hitherto been published, while some are new, having been made during the present year (1907) and based upon the rich material belonging to the Botanical Museum in Copenhagen.

The present notes are the first of a series upon the structure and biology of the Arctic flowering-plants which will probably be published by me and several other Danish botanists; the object of publication is that they may serve as a basis for subsequent botanical studies to those who may work in Arctic countries, and who may thereby be enabled to make biological observations on the spot more quickly and with greater accuracy.

I wish to mention here that when Ekstam in 1894 (p. 419) wrote in regard to me that I "in einer Menge von Fällen nur in Alkohol aufbewahrtes oder getrocknetes Material zu seiner [c: meiner] Verfügung gehabt" as regards the investigations in flower-biology of Scandinavian plants, this is not quite correct, and I never made the above statement. On the contrary, both during my travels in West Greenland in 1884 when, on board a Danish man-of-war, I visited the Danish colonies situated between 64° and 69° N. lat. (Godthaab, Sukkertoppen, Holstensborg, Egedesminde, Jakobshavn and Godhavn) and also during my travels in Finmark, in 1885, when I stayed for a long time at Bosekop, Kaafjord and Tromsø (69°—70° N. lat.) I have always been very careful, above all things, to

study the plants in the field, or at least to carry out my investigations on living material found growing in the open, and to make accompanying pencil sketches; afterwards I drew the published figures from spirit-material, but with continual reference to the notes and sketches made from the living material. In most cases I have investigated the biology of the flowers in their natural habitats.

Almost all the figures have been drawn by myself; this applies more particularly to the flower-biology figures: a few only of the morphological figures have been drawn by others, under my supervision.

This first paper on the morphology of the *Ericineae* and the structure of their flowers will be followed by a second, on their anatomy, by Mr. Henning E. Petersen, Mag. Sc.

Copenhagen, December, 1907.

The species mentioned in the following pages are: -

Andromeda polifolia . . . . . p. 29
Arctostaphylos alpina . . . . . p. 34
— *Uva-ursi* . . . . . p. 39
(*Bryanthus coeruleus* . . . . . p. 17)
(*Cassandra calyculata* . . . . . p. 32)
Cassiope hypnoides . . . . . p. 22
— *tetragona* . . . . . p. 25
Ledum palustre . . . . . p. 6
Loiseleuria procumbens . . . . . p. 13
Lyonia calyculata . . . . . p. 32
Phyllodoce cæruleæ . . . . . p. 17
Pirola minor . . . . . p. 62
— *uniflora* . . . . . p. 63
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Vaccinium Myrtillus . . . . . p. 42
— *Oxycoccos* . . . . . p. 53
— *uliginosum* . . . . . p. 45
— *Vitis-idæa* . . . . . p. 49

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Ord. *Ericaceæ*.

Ledum palustre L.

with f. *decumbens* Ait. and f. *groenlandica* (Oed.). Lange, Conspectus, p. 89.

Kjellman, 1883, p. 505. Warming, 1884, pp. 45, 47, 101. 1885, p. 189, fig. 12, 13; p. 205. 1886 b, pp. 118, 125; 1886—87, p. 110. Poppius, 1903, p. 43. Haglund, 1905, p. 28. Sylvén, 1906, p. 133, tab. IX.

Material from West Greenland and Finmark.

A low shrub, in favourable localities attaining a height of as much as 1 m.; in the Arctic regions often found as a dwarf shrub (usually forma *decumbens*) with prostrate branches, and almost hidden by moss and lichens. The lower part of the stem is prostrate and curving, forming many, usually very slender roots; offshoots may be produced, but propagation by seed appears to be its normal mode of reproduction.

I have not observed runners or stolons with scale-leaves; the growth of the primary root appears to be very strong, and according to Haglund a great number of branches arise more or less irregularly from the base of the primary shoot.

The foliage-leaves remain green two (or three) years; the under sides are densely covered by woolly hairs of a rusty colour. The margins are more or less revolute (Fig. 1). The size of the leaves, both as regards breadth and length varies

considerably under differing conditions of life (see Kjellman, Lange and Warming). According to Haglund the largest leaves occur on basal shoots and on those which have remained for several years in a vegetative condition.

The buds are protected by scale-leaves, and the limit of each year's growth is distinctly marked (Fig. 1). A branch generally requires two or more years to attain the maturity required for flowering. According to Haglund the plant flowers periodically every other year; I have found from two to four years to intervene between the flowering periods.

The plant flowers in spring. The inflorescence is a terminal, many-flowered umbelliform raceme. The flowers are formed during the summer previous to that in which they open, and are enclosed in a terminal bud which is protected by scale-leaves, and is somewhat larger and more globular than are the vegetative buds (Fig. 1 *A* and *D*). Foliage-leaves do not occur on this flowering year's-growth.

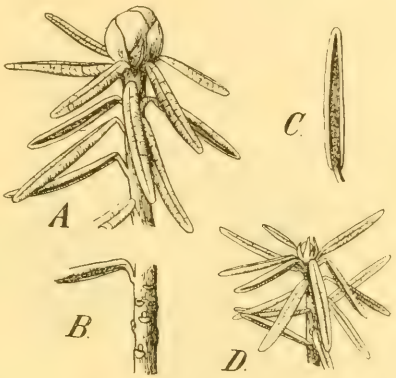

Fig. 1. *Ledum palustre* var. *decumbens* Disko; June 8, 1907 (slightly magn.). *A*, A floral terminal bud. *B*, Portion of a branch with limits of two year's growths. *C*, A leaf, dorsal view. *D*, A branch like *A*, but with vegetative terminal bud. (E. W., 1907.)

After setting fruit the whole of the floral year's-shoot dies. Immediately below it there is developed during the summer either a single branch or several (as many as five), rather closely placed, and often arranged almost in a (spurious) whorl. The rest of the main shoot remains branchless.

The flowers emit a powerful perfume which evidently increases towards night. The question arises whether the strong scent of the whole plant may not be in this as in other cases a guide to insects.

The polypetalous corolla is saucer-shaped, about 1 cm. across (Fig. 2); and white, or more rarely pink. The filaments are white. The flower of the broad-leaved form has five to ten stamens; the number varies because some of the antipetalous stamens, which are always shorter than the antisepalous, are often suppressed; in the flower of the narrow-leaved form (f. *decumbens*), the number of the stamens is generally ten.[1] The filaments are glabrous except in the lower part, a short distance above the base, where they are covered with short projecting hairs (Fig. 2 *B*, *F*); these hairs probably serve to retain the honey. The anthers are glabrous and have no appendages (Fig. 2 *B*, *G*, *H*).

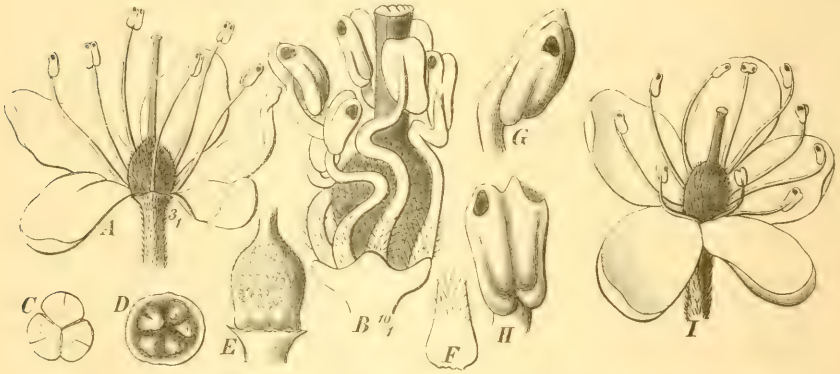

Fig. 2. *A-H, Ledum palustre* f. *groenlandica*; *I, L. palustre* var. *decumbens*. (From West Greenland; July, 11, and 12, 1884.)

A, Open flower. *B*, Stamens and pistil of a completely closed bud; the pores are open. *C*, Pollen tetrad. *D*, Stigma seen from above. *E*, Base of the pistil. *F*, Base of a filament. *G*, *H*, Anthers. *I*, Open flower. (E. W., 1885.)

The plant is protogynous for a short time and then homogamous. The pores at the apex of the anthers are open in the bud while the latter is still quite closed, and while the stamens as yet are highly twisted and lie close to the pistil (Fig. 2 *B*

[1] Unlike Berggren (Fanerogamfloran, p. 856) I have been unable to find any constant difference between the flowers of the narrow-leaved forms and those of the broad-leaved (Fig. 2 *A* shews that of f. *grönlandica*, with 6 stamens and Fig. I that of f. *decumbens*).

G, *H*), consequently, the pollen-grains (Fig. 2 *C*) might be shed at that time, but we can scarcely think that this occurs until the flowers open and the anthers as well as the pollen-grains are dry.

In the full-blown, expanded flower, the stamens are widely spreading (Fig. 2 *A*, *I*), and the stigma is ripe (glistening). The latter consists of five small protuberances seated upon the apex of the style which is flat and has a sharp edge (Fig. 2 *D*).

Self-pollination appears rather difficult unless the wind transfers the pollen to the stigma; in this connection an important feature to note is undoubtedly that the inflorescence comprises so many flowers, and that they occur so closely together that geitonogamy may take place.

Fig. 3. *Ledum palustre*. (From West Greenland.) Ripe capsule in natural position.

Cross-pollination by insects may easily take place, and many kinds of insects are doubtless able to obtain the honey which is secreted abundantly and in large drops at the ten-lobed base of the ovary (Fig. 2 *E*), and is retained by the hairs which occur upon the basal parts of the stamens. In Greenland *Ledum palustre* var. *decumbens* is visited by *Argynnis chariclea* Herbst; but in a garden near Copenhagen I have seen dead or dying individuals of three kinds of flies (most frequently *Empis chioptera* Fall., then *Rhamphomyia hybrida* Zett., and a species of *Microphorus* (*velutinus*?) adhering to it by their wings and legs; the cause of death is unknown; the strong perfume appears to stupefy them. Poppius observed a number of insect-visitors (l. c.).

The ovary is covered with two kinds of hairs, viz. small, shiny, pearl-like glandular hairs, and setaceous hairs (Fig. 2).

As a rule the fruit ripens; this is at least the case in the most southernly and the central parts of West Greenland. The capsule has septicidal dehiscence; the valves open from the base towards the apex and persist, this should be connected with the fact that the capsule is inverted and nods on the curving stalk (Fig. 3).

Rhododendron lapponicum Wahlbg.

Warming, 1885, p. 185, fig. 11; p. 205. Abromeit, 1899, pp. 49, 51. Skottsberg, 1901, p. 15. Dusén, 1901, p. 42. Haglund, 1905, p. 18. Sylvén, 1906, p. 133.

Material from Greenland and Finmark.

A dwarf shrub, as much as 20—25 cm. high; the irregularly branching stems are often much curved. It may also occur as an espalier-like shrub, closely pressed to the ground; in the latter case a great number of dormant buds develop from the axils of the lower leaves, due to the fact that many of the branches die at their apex (Haglund).

The primary root is strong, often thick and irregularly curved. Slender adventitious roots may arise on damp soil, but very sparingly, and the stems do not appear to produce offshoots.

The year's growths are short (from 1 to 3 cm.) and have a few (only as many as 8) closely set leaves (Fig. 6 *E*). The buds are protected by a few arched scale-leaves (Fig. 4); the bud-scars and the limits of each year's growth are distinctly marked. The leaves have been observed to come out in June-August.

According to Haglund the primary shoot lives for a few years and then dies down, and new shoots arise from its base. The branches live 3—4 or more years in a vegetative condition before they flower. They branch but sparingly.

The foliage-leaves remain green on the branches some two years and then fall. Those of the last year are fresher

green in colour than are the older ones, which are more downwardly directed (Fig. 4 *F*).

The flowers, numbering from two to six, are aggregated in a terminal, umbelliform inflorescence which arrests the growth of the branch, and which passes the winter protected by arched scale-leaves (Fig. 4 *F*). The floral buds are larger and more globose than are the vegetative ones (cf. Fig. 4 *A* and *F*). No foliage-leaves occur between the scale-leaves and the inflorescence.

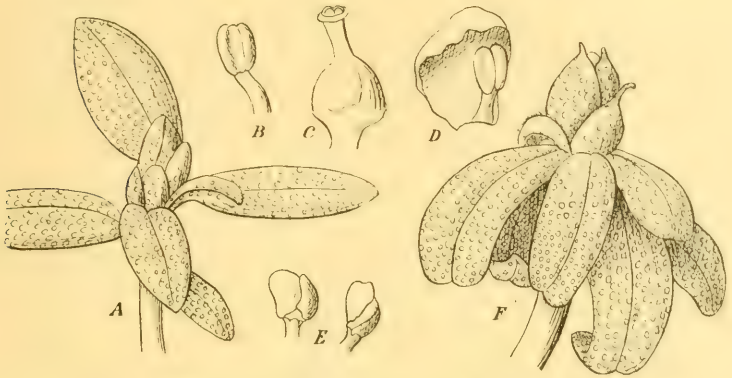

Fig. 4. *Rhododendron lapponicum.* (From Greenland.)
A, Vegetative bud in early spring (June 19, 1887). *F*, Branch with a floral terminal bud (from field in East Greenland bare of snow; Nov. 4, 1891). *B, C, D*, Various parts of its flowers (more highly mag.). *E*, Young flowers from the same floral bud. (E. W., 1907.)

After flowering two or more new shoots arise immediately below the dead apex of the shoot and dichotomy takes place.

The flowers, which have large, thin bracts, scale-like and curved, erect or more or less inclined, are formed during the year previous to that in which they expand and reach in the development of their different parts at least to the stages shewn in Fig. 4 *B—E*.

The corolla is widely bell-shaped (12—17 mm. wide) and purple in colour; in its interior, immediately above its base, it bears a ring of short hairs, probably as a protection to the honey which is secreted by the low, ring-shaped and some-

what lobed disk below the ovary (Fig. 5 *B*, *D*). The hairs which occur at a corresponding height on the swollen part of the filaments (Fig. 5 *E*) may also serve to protect the honey.

Some of the antipetalous stamens are often suppressed so that the stamens of the flowers vary in number from five to ten; and 4-merous corollas may occur together with 5-merous (Fig. 6 *A*, *B*, *C*).

The stamens project beyond the corolla, and are widely spreading so that the anthers are at a distance from the stigma (Figs. 5, 6). They are generally bent downwards towards the front or lower side of the flower. The stamens have no appendages or other projections, but dehisce at the apex by two large pores (Figs. 5, 6).

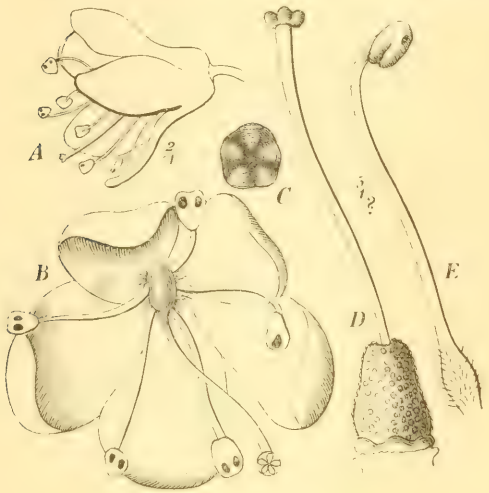

Fig. 5. *Rhododendron lapponicum* (From West Greenland).
A, Flower (2/1). *B*, Another flower, front view (3/2). *C*, Stigma. *D*, Pistil (the style should not have been drawn thicker towards the apex). *E*, Stamen. (E. W., 1885.)

The ovary is covered by peltate glandular hairs as is also the case with the leaves (Figs. 4, 5, *D*); evidently because assimilation takes place in it as in the latter. Generally the style is so long that the stigma stands at the same level as the anthers and cannot touch the latter when they bend inwards towards it (Fig. 5). But it may also happen that the stamens are half the length of the pistil (Fig. 6 *L*).

At Godhavn I found flowers, the stamens of which were short and appeared to have smaller anthers which could scarcely

dehisce and the pollen of which was abnormal (Fig. 6 *G*, *H*). They must be regarded as female flowers.

The style is long and the stigma has 5 protuberances (Figs. 5 *C*; 6 *K*).

The flowers are homogamous or very slightly protogynous; they are evidently adapted for cross-pollination by insects, but self-pollination may also take place. According to Skottsberg they have in Lapland a very strong perfume suggestive of that of the rose.

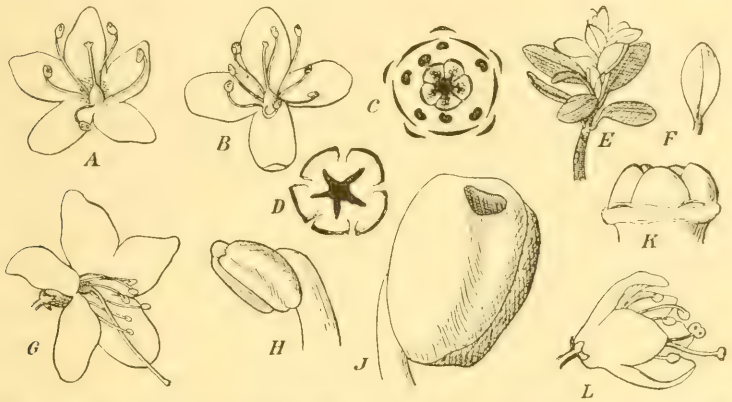

Fig. 6. *Rhododendron lapponicum*. (From West Greenland; July 15, 1884). *A*, *B*, Various forms of flowers (slightly mag.): *C*, Floral diagram. *D*, Diagram of a dehisced capsule. *E*, Branch in spring. F, Leaf. *G*, Flower with sterile stamens. *H*, A stamen of the same; tetrads are developed, but appear to be abnormal. *J*, Normal anther which is open. *K*, Stigma. *L*, Flower with normal stamens. (E. W.)

Pollen may occur in quantities in the open anthers at the same time that the stigma is viscid, and pollen may be found on the stigma of flowers which have not as yet fully expanded.

The plant is chiefly propagated by seed. The capsules ripen both in West and in East Greenland (Angmagsalik).

Loiseleuria procumbens (L.) Desvaux.

Warming, 1885, p. 181, fig. 9, p. 204; 1886 b, p. 126. Lindman, 1887, p. 73. Skottsberg, 1901, p. 16. Haglund, 1905, p. 21. Ekstam,

1894, p. 428. Poppius, 1903, p. 44. Sylvén, 1906, I, p. 132, tab. IX.

H. Müller, 1881, p. 377, fig. 151, and (under the name of *Empetrum nigrum* L.) p. 171, fig. 67. Schröter, 1904, pp. 129—136.

Material from West and East Greenland, Sweden and Norway.

A dwarf shrub with a strong primary root. The branches are more or less prostrate (Fig. 7 *C*), their lower parts are often hidden by moss and other plants and covered by soil; they may attain to a thickness of about one centimetre and are more or less curving. Roots often arise from the stem especially on damp soil, but they are generally hair-like; they may however become strong and then new plants may arise.

Fig. 7. *Loiseleuria procumbens.* (From West Greenland.)
A, Part of a shoot showing the mode of branching, *I* signifies the main axis, and *II* a lateral axis of the 1st order. *B*, A similar shoot: to the leaf *a* belongs the branch *ag*; to *b*, *bg*; to *c*, *cg*. *C*, A flowering branch (reduced one-half). (E. W., 1907.)

According to Hagluno and Sylvén the primary shoot dies in the second year or later (after 4—5 years) and is replaced by strong lateral shoots.

The year's shoots are branched; the first internode of the branches of the first order (II) is elongated (Fig. 7). Scale-leaves are absent, but the basal parts of the leaves are erect and protect the young parts which occur between them (Fig. 7). The leaves live a couple of years (according to Hagluno three years) and after death may sometimes persist for a long time, black and decaying upon the branches, before they crumble away and turn into mould; but as a rule they disappear quickly.

The branches sometimes continue growing for several years before they are stopped by an inflorescence. At the

end of the floral branches from two to four flowers arise from the axils of bracts, or the two lower ones may occur in the axils of foliage-leaves. Each flower has two bracteoles at its base (Fig. 8 *E*, *C*). Between the flowers the abortive apex of the main-shoot may be observed (Fig. 8 *D*).

The same plant appears sometimes to flower several years in succession; the flowering plants have often only two pairs of foliage-leaves on the shoots and are extremely rich in flowers.

After fructification the flowering part of the shoot dies and branches arise from the axils of the foliage-leaves which occur

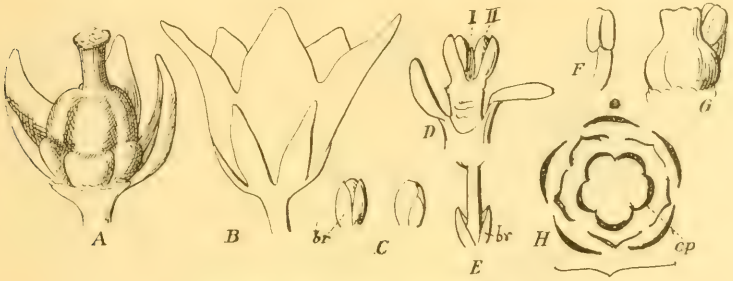

Fig. 8. *Loiseleuria procumbens.*

A Pistil and part of the calyx (from West Greenland). *B*, Shews the form of the open flower (West Greenland); about $^5/_1$. *C*, a flower-bud with its two bracteoles (*br*). *D*, Apical portion of a branch; on each side of the dead apex of the shoot (*I*) which had borne a flower, occur two buds (*II*) in the axils of the two uppermost leaves (Upernivik; Aug. 30, 1886). *E*, Flower-stalk with its two bracteoles (*br*). *F*, *G*, Parts of a flower-bud (Iceland; Sept. 10). *H*, Diagram of calyx, petals, and carpels (*cp*). (E. W., 1907.)

immediately below so that the branching becomes dichotomous.

In favourable localities great numbers of adventitious shoots are formed (Hagluno).

The median petal is anterior. The carpels are antipetalous when they are of the same number as the petals (Fig. 8 *H*), but often they are fewer in number. 4- or 6-merous flowers are sometimes met with.

The flowers are formed during the year previous to that in which they open, and by the beginning of winter have large pistils and stamens (Fig. 8 *F*, *G*).

All the parts of the flower are glabrous. The flowers

(Fig. 8 *B*) are not fragrant, but they bloom a very long time. The corolla is brilliantly coloured, rose-red or crimson. The Greenland and Scandinavian specimens (Fig. 9 *A*) — as also those from Switzerland, according to H. Müller — are from 4·5 to 6 mm. in diameter. I have seen specimens from the north of Sweden measuring as much as 7 to 8 mm. in diameter (Fig. 9 *F*).

The corolla falls off without carrying the stamens with it.

In Greenland the flower is at first protogynous for a short time, and then a long homogamous period ensues. This is also

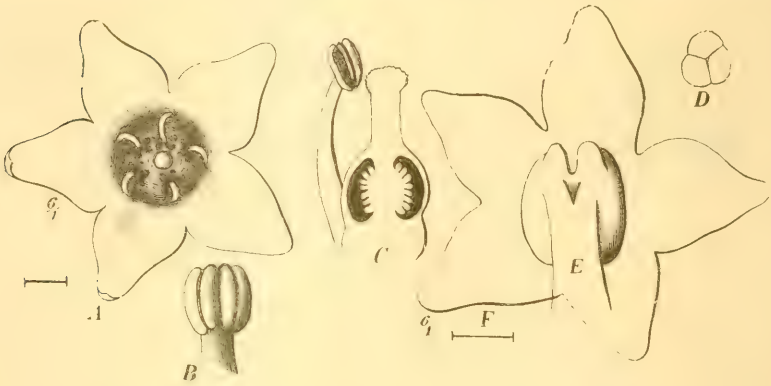

Fig. 9. *Loiseleuria procumbens.* (From West Greenland.)
A, Flower seen from above. *B*, Stamen (10/1). *C*, Pistil in longitudinal section, and a stamen (10/1). *D*, Pollen tetrad. *E*, Anther seen from the dorsal side (26/1). *F*, Outline of a corolla. (E. W., 1885.)

the case in Scandinavia, Nova Zembla, and in the Alps (Warming, Lindman, Ekstam, Ricca, and H. Müller). According to Lindman the female stage begins even in the bud. In Italy the flower is, according to Ricca, markedly protogynous.

H. Müller is of opinion that spontaneous self-pollination can only occur when the flowers close in unfavourable weather, or remain closed, for under other conditions the anthers are too far from the stigma (Fig. 9 *A*). In Greenland the weather appears to have very little influence on the flower as the stamens in rainy weather at most curve perhaps slightly more inwards towards the

pistil. During rain the flowers may be filled with water. But judging from Müller's figure, the anthers in the Greenland and the Scandinavian specimens appear on the whole to stand closer to the pistil than in the Alpine specimens; sometimes even they are in direct contact with it (Fig. 9 *A*); the stamens are more erect than those in the plants from Central Europe, or they may even be curved inward; so that spontaneous self-pollination is inevitable. Lindman also mentions movements of variation and self-pollination, but Ekstam did not observe any such movements, he even refers it to "Alpenpflanzen bei denen immer die Narben mit dem Blütenstaube der eigenen Staubbeutel bestreuet auftraten."

In Greenland, honey is secreted abundantly by the ring-shaped, lobed nectary at the base of the ovary (Fig. 8 *A*).

In Greenland I have seen small flies in the flowers; "at the top, near the region of snow" Wormskiold observed a butterfly sucking at one of the flowers, so cross-pollination appears sometimes to take place.

The fruit ripens in East and West Greenland and in Finmark. But the fruit formed does not always ripen the year the plant flowers, in which case it appears to perish. After the corolla has fallen off the calyx closes round the ovary.

Phyllodoce coerulea (L.) Gren. & Godr.

Phyllodoce taxifolia Salisb. *Bryanthus coeruleus* (L.) Dippel.

Warming, 1885, p. 170, figs. 3, 4; p. 203; 1886 a, p. 19. Lindman, 1887, p. 72, tab. IV, fig. 39. Ekstam, 1897, p. 428. A. Cleve, 1901, p. 43. Skottsberg, 1901, p. 12. Poppius, 1903, p. 43. Haglund, 1905, p. 13. Sylvén, 1906, p. 132.

Material from Greenland, Norway (Finmark) and Sweden.

An evergreen dwarf shrub; the branches are more or less prostrate and produce slender roots, generally few in number; according to Haglund they occur abundantly on damp soil.

The primary root is strong; the adventitious roots may sometimes also become strong, and then new plants may be produced by their agency (Haglund). Dormant buds occur.

According to Haglund the primary stem grows monopodially for some years, then it dies and is replaced by new shoots which arise from the base; these shoots die after a period of three to four years and are replaced by three to four new shoots near the apex (compare also Sylvén).

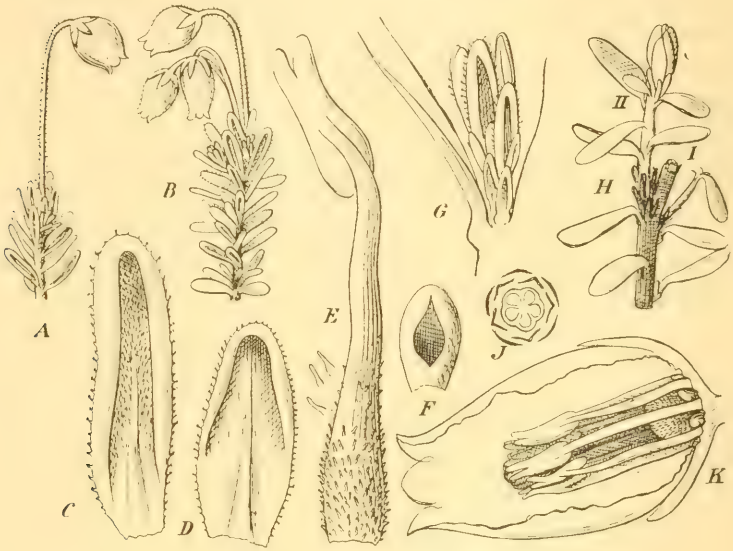

Fig. 10. *Phyllodoce coerulea* (*Bryanthus coeruleus*).
(From West Greenland; July 7, 1884.)

A, B, Two branches with flowers (West Greenland; July 5, 1884); slightly reduced. *C*, A leaf in dorsal view; length 9 mm. *D*, A leaf which has a flower situated in its axil. *E*, Stamen with short hairs upon it; and some hairs from it more enlarged. *F*, Valve from a capsule seen from the inner side. *G*, A leaf-bud in the act of opening (July 6, 1884). *H*, Branch in spring; *I* and *II*, shoots of different order. *J*, Diagram of flower (the stamens omitted). *K*, Longitudinal section of a flower. (E. W.)

Not until then, and therefore when it is several years old, does it appear that the plant flowers. According to Haglund the buds are naked, but I am of opinion that the short, brown and somewhat erect leaves, which usually decay quickly, and which occur at the base of each year's shoot and are

instrumental in marking the limits of each year's growth fairly distinctly, ought strictly speaking to be called scale-leaves (see Fig. 10 *G*, *H*). The year's growths are rather short, only from one to two cm. long.

According to Hagluno assimilation may take place in the foliage-leaves for several years, but no definite proof of this has been given. In Greenland I found three-years-old leaves which were still green.

The flowers, numbering from one to six, are situated at the apex of the branches (Fig. 10 *A*, *B*); they spring from the axils of the foliage-leaves which occur immediately below the rudimentary uppermost parts of the branches. After flowering the whole of the floral portion of the shoot dies. The leaves, which subtend the flowers (Fig. 10 *D*) are relatively broader than the other foliage-leaves (Fig. 10 *C*; Fig. 11) and a smaller portion of their margin is rolled back.

Fig. 11. *Phyllodoce coerulea* (*Bryanthus coeruleus*) A leaf seen from the dorsal side. (E. W., 1887.)

The flowers have two thin bracteoles at the base of their stalk (Fig. 12 *H*).

After the floral portions of the shoots have died, two to several new foliage-bearing shoots arise in the axils of the leaves immediately below them.

There is a certain periodicity in the plant's flowering, and this is the case with the plants in the whole of the district in question. Thus the species flowers sparingly or scarcely at all during certain years, and then there follows a year rich in flowers (Hagluno).

The flowers are formed during the year previous to that in which they open.

The following I find to be the "flower-biology;" the account differs considerably from that of Axell (1869).

In Greenland the flowers are among the earliest spring flowers, they are very conspicuous, being raised into the

air on long stalks (Fig. 10). The violet-purple, urceolate corollas, which are covered with red glandular hairs, usually turn their throats downwards (Figs. 10, 12). I have found the flowers to be scentless (Bessels mentions them as fragrant). They are 9 to 11 mm. in length.

The flower is protogynous for a short time (Greenland and Finmark), and then becomes homogamous (as also observed by Lindman and Ekstam). Even in the bud, while the anthers are still

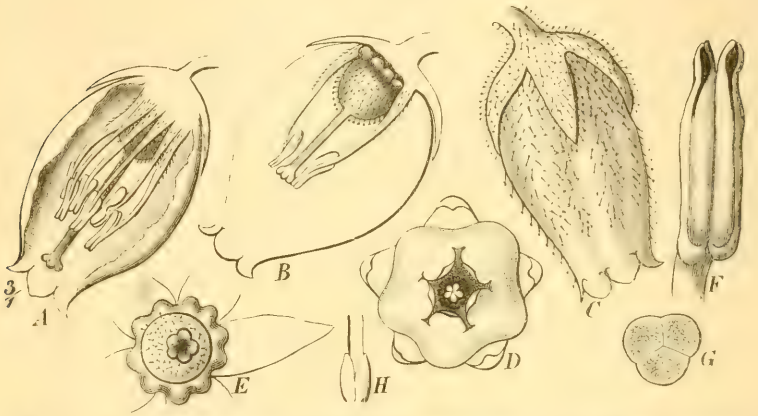

Fig. 12. *Phyllodoce coerulea* (*Bryanthus coeruleus*). From West Greenland. *A*, A young flower which has just expanded; only two of the anthers have opened; pollen already seen upon the stigma (July 6, 1884). *B*, A flower the anther and stigma of which are at the same level. *C*, A third flower, also young, newly expanded, in which, as in *B*, the pores and stigma occur at the same height, 1/3 to 2/3 that of the corolla; the anthers are full of pollen; only the long stamens are open; quantities of pollen occur upon the stigma. *D*, The same flower as *C*, seen from above; the glandular hairs are omitted. *E*, The pistil and the nectary seen from above. *F*, Anther. *G*, Pollen tetrad. *H*, Base of the flower-stalk with the two bracteoles. (E. W., 1885.)

closed, the five-lobed stigma (Fig. 12 *E*) is glistening and viscid; but immediately upon the slight expansion of the corolla the anthers on the longest stamens may be found to have dehisced and the pollen-tetrads (Fig. 12 *G*) to have been shed upon the stigma. There are two elongated pores at the apex of the anthers (as shewn in Fig. 12 *F*) which have no appendages.

The pollen may be so dry and may lie so loosely in the anthers that when the flowers are shaken slightly it flies out

of the latter as clouds of dust. I very often found shed pollen upon the inner parts of the flower. Self-pollination must undoubtedly take place easily because the anthers always stand around the style with their pores turned towards the stigma which is below or almost on the same level with them (Fig. 10 *K*: Fig. 11 *A*). Almost all the tetrads I found on the stigma occurred at its edge. The normal arrangement seems to be for the anthers to stand immediately below the stigma or around it.

I find that both in Greenland and in Finmark some variations occur in the relation between the stamens and the pistil, as also may be seen from the figures. The stigma may occur from 1 to 2 mm. above the anthers. But I have not found the anthers to stand as close to the stigma in the European as in the Greenland flowers (Fig. 10 *K*). These differences in the relative length of the organs in question do not seem to depend upon the age of the flower; the anthers appear however to stand closer to the stigma in the young flowers than in the older ones. Lindman has also noticed these variations, and has observed the stigma to be situated even lower than the base of the anthers (l. c. p. 72).

The flower is also distinctly adapted for cross-pollination by insects. This may take place easily when an insect thrusts its proboscis through the narrow throat of the corolla down to the honey, which is secreted by a yellow, ten-lobed nectary (Fig. 12 *E*). The filaments are hairy at their bases, the hairs serving in this as in other cases to retain the honey in the drooping flower (Fig. 10 *E*; Fig. 12 *A*).

We may assume humble bees to be among the insect-visitors. In Finmark I saw them visit the flowers, and on the Dovre Lindman saw *Bombus alpinus*, in Lapland Skottsberg *Bombus serimshiranus* D., in Varanger Poppius *Bombus lapponicus* Fabr. and *B. nivalis* Dheb. do so. In Finmark I often observed styles and stamens which had been bitten off by ants.

After fertilisation the corolla falls off and the calyx with

its glandular hairs closes on the ovary, which is also covered with glandular hairs.

The fruit, which is a septicidal capsule (Fig. 10 *F*), ripens both in West and East Greenland. It is seated upon an upright, straight stalk.

The carpels are antipetalous (Fig. 10 *J*) and the lobes of the stigma antisepalous; the arrangement of the parts of the flower is the same as in the Ericaceæ.

Cassiope hypnoides (L.) Don.

Warming, 1885, p. 170, figs. 7, 8; 1886—87, p. 113. Lindman, 1887 a, p. 71, tab. III, fig. 37. Ekstam, 1894, p. 428. Abromeit, 1899, p. 49. Skottsberg, 1901, p. 12. Haglund, 1905, p. 26. Sylvén, 1906, p. 131.

Material preserved in spirit, and observations from Greenland and the north of Scandinavia.

A creeping dwarf shrub with a strong primary root. The prostrate, woody stems, which are often covered by moss and soil, frequently give off many very slender, but much branched roots. Hence it may spread over large patches of ground and break up into independent plants. The stems branch sparingly, generally with one to two branches from the upper part of the year's shoots, especially when the latter produce flowers. But owing to the shortness of the year's shoots numerous branches often occur crowded together into dense cushions.

The buds have no scale-leaves, but the year's shoots have small foliage-leaves at their bases, the limits of each year's growth are therefore not distinctly marked.

The stems are slender (usually about 1 mm. thick), but may attain to a thickness of 4 mm. The wood of an 11-years-old branch, according to Haglund, was only 1·25 mm. in diameter, its largest annual ring being 0·25 mm.

The foliage-leaves are more or less erect (Figs. 13, 14); they remain several years on the branches, but very possibly

are unable to perform their functions for more than two, or at the most three, years. In exposed, dry situations the older leaves often become quite colourless.

The flowers occur singly at the apex of the branches, and are drooping (Fig. 13). The leaves at the base of the peduncles are shorter and broader, and more scale-like than the usual foliage-leaves (Fig. 14 *F*). The flowers are formed in the bud during the year previous to that in which they expand (Fig. 14 *B*). The calyx and peduncle are deep-red in colour.

The bell-shaped corolla is white with purple teeth and is widely expanded, hence no hairs occur upon its interior (Fig. 15).

Fig. 13. *Cassiope hypnoides.* Part of a plant; 2/1. (E. W., 1885).

Above their slender bases the filaments become very thick (being broader than those in *C. tetragona*), and are covered with small pointed warts (Fig. 15 *F*); they stand close to the ovary, with their long, hairy appendages directed straight outwards (Fig. 15 *A*, *B*). The pores are elongated (Fig. 15 *E*, *F*); at first they turn downwards, afterwards upwards (consequently in the drooping flower downwards). Lindman points out that the appendages must be shaken before the pollen (Fig. 14 *C*) can be shed.

The style is conical and very thick at the base (Fig. 15 *C*). The carpels are antipetalous, and the flower is obdiplostemonous.

In the material from Greenland the apex of the style is evenly rounded off so that the stigma is not very prominent (Fig. 14 *E*; Fig. 15, *A*, *C*). Lindman and Ekstam found the latter to be more distinct, occurring as a flat, somewhat rough disk.

The flower is homogamous or perhaps protandrous for a

short time (Warming, Ekstam), according to Lindman protogynous-homogamous (Norway, the Dovre).

As the anthers dehisce in the still incompletely open flower, and the stigma may also be shiny, pollination will, in all probability, take place immediately the flower expands (Fig. 14 *D*). Pollen is at that time seen shed and lying on the inner parts of the flower.

Honey is secreted by the slightly lobed, ring-shaped disk at the base of the ovary (Fig. 15 *C*) and appears to be retained there between and outside the basal parts of the stamens;

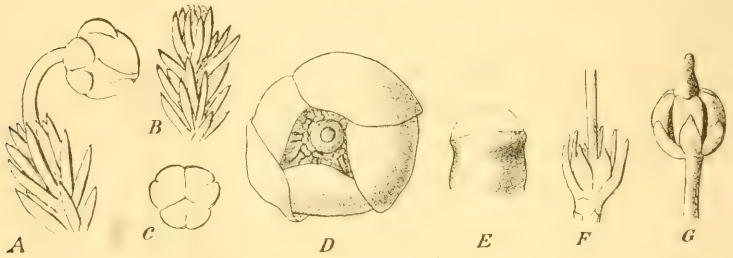

Fig. 14. *Cassiope hypnoides.*

A, The flower still in a bud; 3/1 (Disko; July 20, 1884). *B*, A flower is within the bud (Upernivik; Sept. 2. 1886). *C*, Pollen tetrad. *D*, Even in a flower of this age the anthers are open, and the pollen has fallen out (Disko; July 22, 1884). *E*, Apex of the style shewing stigma covered with mucilage. *F*, Base of a peduncle with the surrounding leaves (those in front have been removed). *G*, Capsule. (E. W.)

in effecting this the small warts on the filaments (Fig. 15 *F*) most probably play a part.

Self-pollination as well as cross-pollination by insects appears to be able to take place. According to Skottsberg the flowers are slightly fragrant in Lapland and are visited by *Bombus lapponicus*.

The plant sets ripe fruit in East and West Greenland, in Iceland and in Scandinavia (Fig. 13; Fig. 14 *G*). In West Greenland I have seen specimens which had abundant fruit from the previous year, but were barren in the present year. Norman and Haglund have made similar observations; therefore it may be assumed that flowering and barren years alternate.

After flowering the pedicel rises straight into the air and the sepals close round the valves of the fruit (Fig. 13; Fig. 14 *G*).

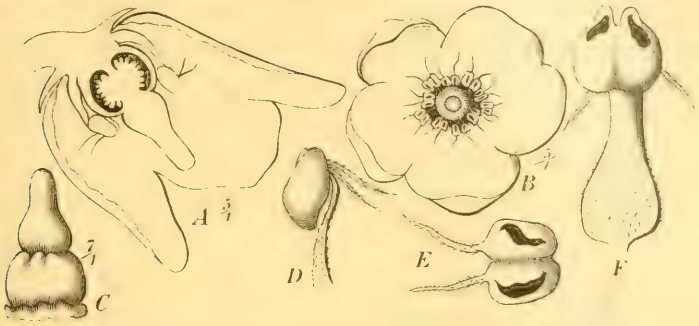

Fig. 15. *Cassiope hypnoides.* (From West Greenland.)
A, Flower in longitudinal section. *B*, Flower seen from above. *C*, Pistil with the slightly lobed nectary. *D*, *E*, *F*, Stamens. (E. W., 1885.)

Cassiope tetragona (L.) Don.

Warming, 1885, p. 175, figs. 5, 6; p. 203; 1886 b, p. 118; 1886—87, p. 108, fig. 2. Ekstam, 1898, p. 9. Abromeit, 1899, p. 48. Andersson & Hesselman, 1900, p. 43. Haglund, 1905, p. 24. Sylvén, 1906, I, p. 130, tab. IX.

Material preserved in spirit from Greenland, Spitzbergen and Finmark; observations from Greenland and Finmark.

A dwarf shrub of the *Calluna*-type. The older stems, which attain, although rarely, to a length of from 1/2 to 1 metre, are prostrate and form extremely slender and abundantly branching roots; they are often overgrown by mosses, lichens and other plants as also covered by soil. The plant has a strong primary root which keeps alive during the whole of its life, while the adventitious roots are not of much importance. The present species is chiefly or almost exclusively propagated by seed. The primary shoot has been described by Sylvén. The cotyledons are oval. The primordial leaves and the second year's leaves are flat. After that the leaves gradually attain the well-known form which is shewn in my figures 16 and 17 and in Henning E. Petersen's figure.

The growth of the stem is monopodial, the flowers occurring singly in the axils of leaves (Figs. 16, 17), the lateral branches are few in number, being developed generally from the basal parts of the year's shoots, and especially below floral year's-shoots (Fig. 16 *G*); they often arise from the axils of opposite leaves and are therefore themselves opposite (Fig. 17 *C*). The limits of each year's growth are not distinctly marked, scale-leaves being absent from the winter buds (Fig. 16 *A*, *E*), but the year's

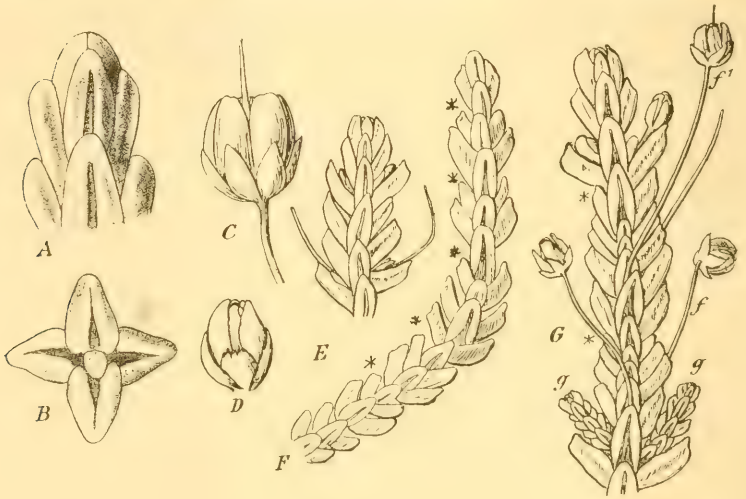

Fig. 16. *Cassiope tetragona*. (From West Greenland.)

A, Apical part of a branch (Upernivik; July 30, 1887). *B*, Transverse section of a branch shewing the decussate position of the leaves. *C*, Capsule (about $^3/_1$). *D*, the flower for the next year is already formed (Godhavn; June 14, 1907; 200 m. above the level of the sea). *E*, Apical part of a branch with flowers formed in its upper part; about $^2/_1$ (Godhavn; June 14, 1907). *F*, *G*, Branches shewing several year's growths (the asterisks indicate their limits). *G*, A shoot with lateral branches, *g* and g^1, and fruits (*f* and f^1) from the two previous years (about $^2/_1$).

growths have at their base only foliage-leaves, which are smaller, though only slightly so, than are the other foliage-leaves; therefore the shoots are distinctly thinner at the limits of each year's growths (Fig. 16 *F*, *G*). The lateral buds are protected by the subtending leaves. The lateral shoots are often dwarf shoots.

The foliage-leaves on each year's shoot number from about eight to twenty-four. They remain green two to three years.

but persist in a decaying and colourless condition for many years (Fig. 17 *C*).

The flowers occur laterally upon the lower part of the year's shoots; each has four bracteoles at the base of its stalk (Fig. 18 *C*; Fig. 16 *D*). They are obdiplostemonous and the carpels are antipetalous. They are formed during the year previous to that in which they open, and pass the winter in a fairly well-developed condition (Fig. 16 *D*, *E*; Fig. 17 *C*).

The same shoot may flower several years in succession (Fig. 16 *G*).

The corolla is yellowish-white and emits a perfume, which recalls that of the Lily of the Valley (*Convallaria majalis*), but is not powerful, and is strongest in the evening. It is bell-shaped and nods with down-turned throat on its curving stalk (Fig. 17). Its length is from 7 to 8 (8·5) mm.

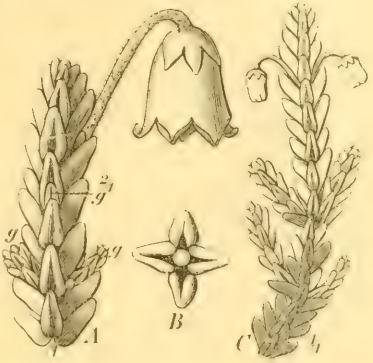

Fig. 17. *Cassiope tetragona*. (From West Greenland).

A, A branch with flower; *g*, new lateral shoot: *B*, The same in transverse section. *C*, A branch recently cleared of snow (July 12, 1884); the dark leaves are dead. (E. W., 1885.)

The length of the pistil is about $^3/_4$ of that of the corolla, and the stigma is situated almost at the throat (Fig. 18 *A*). The anthers, as illustrated in Fig. 18 *A*, stand at about the middle of the corolla. The filaments are only slightly thicker at their bases than at their apices (Fig. 18). The anthers are black: their pores are elongated, turned upwards, and are open even in the bud. The appendages which are long and slender, are covered with small, stiff hairs (Fig. 18 *B*); they spread horizontally from the anthers and reach well towards the sides of the corolla, so that an insect on thrusting its proboscis into the latter in search of the honey which is secreted by the yellowish-coloured disk below the ovary (Fig. 18 *A*, *D*), must

inevitably touch them and thereby scatter the pollen tetrads, of this we may easily convince ourselves by experiment.

On examining flowers in the fields I have found masses of pollen shed upon anthers, style and stigma.

The plant is at first protandrous for a short time and then homogamous. Self-pollination may easily take place, and very early, owing to the position of the stigma below the anthers. Even in completely closed flowers the anthers were found open, and the corolla, anthers, style and stigma were covered with

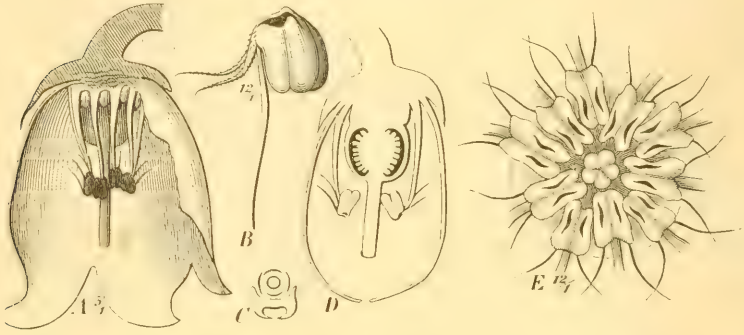

Fig. 18. *Cassiope tetragona.* (From West Greenland.)
A, Open flower. *B*, Stamen. *C*, Diagram of a leaf with a flower in its axil, and its four bracteoles. *D*, Even in such a bud the anthers are open and partly filled with air, but the pollen is not yet shed. *E*, Shews the position of the anthers and of the stigma. (E. W., 1885.)

pollen. In Fig. 18 *D* the pores are already open and the anthers are dry, but the pollen is not yet shed.

The stalk of the capsule is erect (Fig. 16 *G*). Ripe fruit is produced in great quantities in West and East Greenland, Iceland, Spitzbergen, the north of Scandinavia and at St. Lawrence-Bay, but many flowers are also met with which appear to have withered without setting fruit.

According to Haglund the fruit doubtless ripens under the snow or during the following spring. The capsule has loculicidal dehiscence.

Andromeda polifolia L.

Warming, 1886, p. 18, Fig. 6. Lindman, 1887, p. 70. Kihlman, 1890, p. 155. Ekstam, 1894, p. 427. Poppius, 1903, p. 43. Sylvén, 1906, I. p. 129.

Observations and material from West Greenland; Tromsö (Norway); Denmark.

An erect, evergreen dwarf shrub (about 3—4 dm. high), sparingly branched; the slender, far-reaching subterranean runners have long internodes, bear scale-leaves, and have a straight apex (Fig. 19 *A*, *D*). The roots given off by the runners are very slender and abundantly branched; they arise from the axils of the leaves (Fig. 19 *B*, *E*).

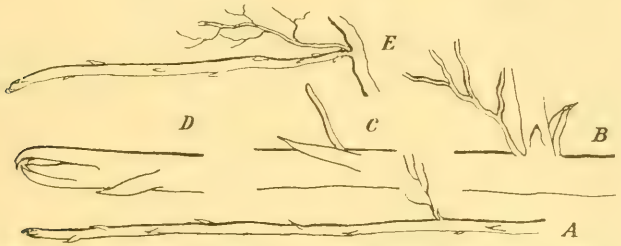

Fig. 19. *Andromeda polifolia.* (From Denmark; Aug. 5, 1887.)
A, Runner. *B*, Portion of a runner shewing a branch and a root both situated in the axil of a scale-leaf. *C*, A similar runner. *D*, The apex of a runner. *E*, Portion of a runner shewing a branch with a root above. (E. W., 1907.)

The year's shoots have scale-leaves at their bases. The axillary buds are partly protected by the erect petioles (Fig. 20 *A*). The more vigorous of the lateral shoots arise from the axils of the uppermost leaves, i. e. those below the terminal inflorescence, and the uppermost shoot often forms a sympodium together with the parent stem.

The leaves are coriaceous and articulate, and remain fresh throughout at least one winter; they are strongly glaucous beneath and have revolute margins (Fig. 20 *A*).

The flowers are few in number (from one to five) and occur on long red stalks in an umbelliform raceme; they are secund and drooping. The lowermost may be in the axils of

foliage-leaves, the uppermost in those of scale-leaves (Fig. 21 *B*). Two bracteoles are seated at the base of each stalk (Fig. 21 *A*). The flowers are formed during the year previous to that in which they open, and pass the winter protected by foliage or by scale-leaves (Fig. 20 *A*, *B*, *C*). In structure the flowers resemble most closely those of *Arctostaphylos Uva-ursi*. The corolla is rose-red, roundly-urceolate, and 5-angled and turns its narrow throat downwards (Fig. 21 *B*); the calyx also is rose-coloured. The interior of the corolla is covered with erect, usually somewhat upturned hairs which extend to the margin of the limb (Fig. 21 *C*, *D*); its length is from 4 to 6·5 mm.; it continues to grow during flowering.

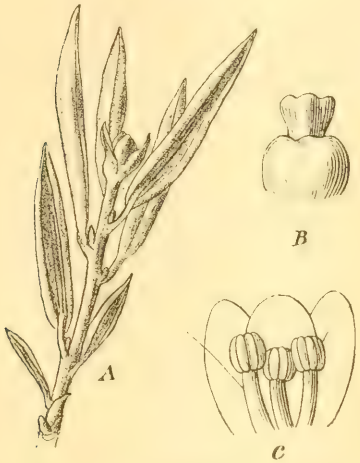

Fig. 20. *Andromeda polifolia*.
A, Branch with terminal bud which encloses flowers for the next year (Denmark; Aug. 5); slightly mag. *B*, Pistil from this bud. *C*, Part of a flower shewing stamens and corolla of the same bud. (E. W.)

The relative length of the different parts of the flower is shewn in Fig. 21 *C*. The stigma is situated just at or immediately within the throat of the corolla, and the anthers which are at the level of the middle of the pistil and the corolla, bend inwards towards the style. The filaments are strongly swollen just above their slender, short bases, and are covered with fairly long hairs along the greater part of their length (Fig. 21 *G*). Here, as is often the case, they probably serve to retain the honey, secreted by the disk at the base of the ovary (Fig. 21 *G*).

The anthers are covered with small protuberances (Fig. 21 *E*): they open at the apex by two pores of irregular shape. The two appendages are glabrous and slant upwards and outwards (Fig. 21 *C*, *E*, *G*).

The stigma is not always distinctly lobed, but sometimes there are five small, rounded projections upon it (Fig. 21 *H*, *I*) covered by a thick mucilage which it secretes.

The plant is homogamous (Warming, Lindman, Ekstam). The pores of the anthers are open even in the bud, and the pollen grains (tetrads, Fig. 21 *F*) lie loose in the pollen-sacs: however, I have not found the pollen shed until the corolla is open and the anthers have become dry. Even in the bud the stigma may be seen to be shiny and very viscid. Self-pollination may

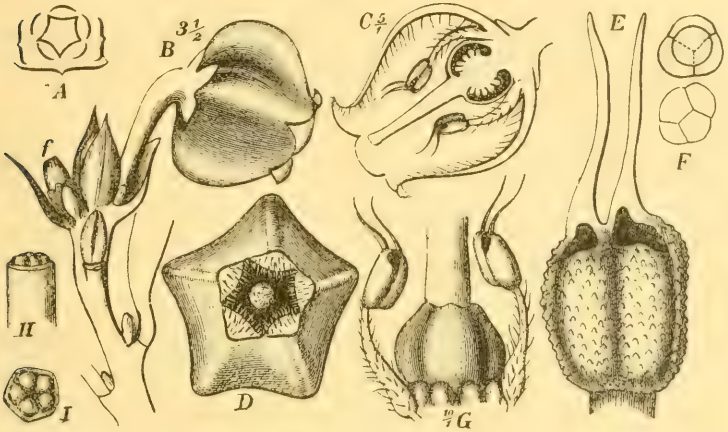

Fig. 21. *Andromeda polifolia.* (From Denmark; May 18.)

A, Diagram of the outer leaves of the flower and of the bracteoles. *B*, Apex of a flowering branch with the two lowest foliage-leaves which protect small vegetative buds; above them a foliage-leaf, which has been removed, protected the most vigorous of the vegetative buds; above this two bracts are seen, one protecting a flower that has not expanded (*f*), and another protecting an expanding flower; some closely-set scale-leaves terminate the branch. *C*, Longitudinal section through a fully expanded flower. *D*, A flower seen from above. *E*, Anther. *F*, Pollen tetrads. *G*, Ovary with the nectary and two stamens. *H*, *I*, Apex of the style, and stigma. (E. W., 1886.)

easily take place in the recently expanded flower, because its stigma is situated immediately below the anthers and it almost closes the throat, which is only from 1·25 to 1·5 mm. wide (Fig. 21 *D*). The hairs on the corolla may serve temporarily to retain the shed pollen-grains In Finmark I found masses of pollen-grains adhering to the hairs in the throat (July 3. 1885).

Sometimes, however, the hairs on the inside of the corolla, especially those at the throat, occur rather sparingly.

Cross-pollination by insects may easily take place. Honey is secreted by a hypogynous disk of ten glands (Fig. 21 *G*). The capsule is erect. Poppius observed *Colias Palæno* L., *Plusia microgamma* Hb. and *Bombus agrorum* Fabr. visiting the flowers.

The flower is obdiplostemonous, and the carpels are antipetalous. I have found 4-merous flowers in Finmarken and in Greenland.

I do not find any important difference between Greenland and European individuals.

Lyonia calyculata (L. Don.); syn. *Cassandra calyculata* (L.) Don.

Haglund, 1905, p. 33. Warming, 1906, III, p. 150.

Material from Finland (flowering in the Botanic Garden in Copenhagen).

A low, erect shrub. The coriaceous leaves remain for more than a year on the branches, and turn reddish in colour in the autumn. The buds, which are protected by scale-leaves are still small even in autumn.

The flowers, which are white, occur singly in the axils of the upper leaves, and are drooping. Towards the apex of the shoots they rather cluster together, and the subtending leaves becoming smaller they approximately form a racemose inflorescence. Two ovate-acute bracteoles occur immediately below the calyx of the flower (Fig. 22 *C*).

After flowering, the whole of the floral portion of the shoot, i. e. about one third to one half of the whole of the year's shoot, dies, and then just below it long shoots, from one to several, all similar in appearance, are developed while the lower part of the shoot remains branchless.

The corolla is cylindrical-urceolate, about 7 mm. long; and

the throat is relatively wide, about 1·5 mm. across. The interior of the corolla is glabrous (Fig. 22 *C*, *H*).

Although the stigma is situated in the throat (Fig. 22 *H*) or sometimes even beyond it, the anthers reach only to the middle of the corolla or somewhat higher, yet the pores by means of which they open are not far from the stigma beneath them. The stamens have no bristles nor appendages, but the anthers and filaments are rough with small protuberances (Fig. 22 *D*, *E*).

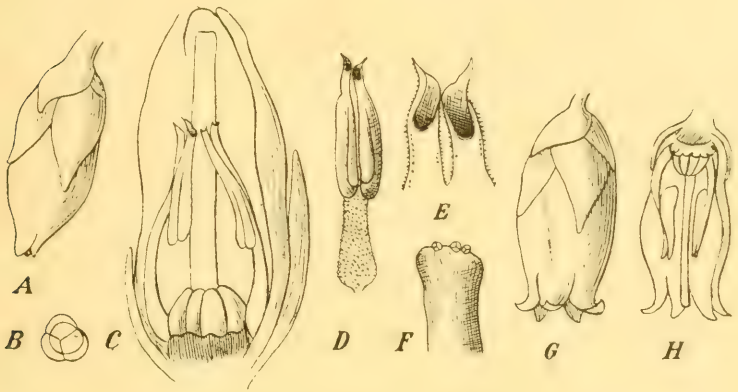

Fig. 22. *Cassandra calyculata.*

A, Even in such a bud the pollen has fallen in quantities out of the anthers and is seen to lie upon the glabrous sides of the corolla (about $^4/_1$). *B*, Pollen tetrad. *C*, Longitudinal section through a young flower. *D*, *E*, Stamen and upper part of anther of *C*. *F*, pollen tetrads upon the stigma of a bud. *G*, Flower; *H*, the same in longitudinal section. (E. W.)

Self-pollination appears to be able to take place easily. The plant is doubtless homogamous; even in the bud quantities of pollen-grains (Fig. 22 *B*) fall out of the anthers and are seen to lie upon the inside of the corolla as also upon the stigma (Fig. 22 *A*, *F*).

At the base of the ovary there is a honey-secreting disk, dark-green in colour and ten-lobed (Fig. 22 *C*).

In the Botanic Garden in Copenhagen it flowers early, even in the month of March.

Arctostaphylos alpina (L.) Spreng.

Warming, 1885, p. 206; 1886 a, p. 13, fig. 5. Ekstam, 1897, p. 187. Ambronn, 1891, p. 70. Skottsberg, 1901, p. 11. Haglund, 1905, p. 34. A. Cleve, 1901, p. 42. Poppius, 1903, p. 43. Sylvén, 1906, I, p. 129.

Schröter, C., 1904, Pflanzenleben, p. 157.

A prostrate dwarf shrub, with a strong primary root. The long, prostrate shoots form adventitious roots, which may grow very strong, and therefore the plant may produce off-shoots, which become detached from the parent and form independent plants. The older branches are closely pressed to the ground, and often more or less subterranean and hidden under decaying leaves or other plants.

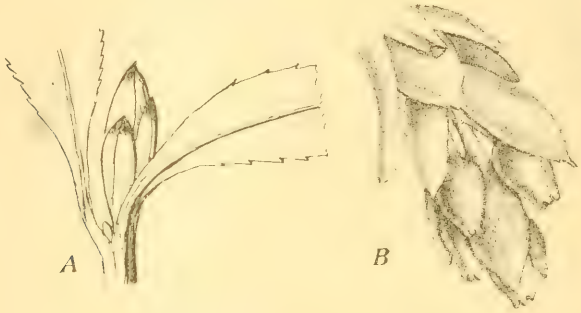

Fig. 23. *Arctostaphylos alpina.*
A, Terminal bud (Norway; Aug.). *B*, Young inflorescence (Finmark; July 7, 1885); all the parts of the flower are formed, and are fairly large.

The foliage-leaves turn deep red in autumn, and then decay, but persist a very long time in the faded and decayed condition until they crumble away. They have a peculiar silvery lustre owing to the fact that the two lowest layers of cells, by separating from the others, form a hollow space inside the leaf filled with air.

The buds are protected partly by the petioles which are somewhat erect at the base and adpressed to the stem, and partly by true scale-leaves (Fig. 23 *A*). The terminal buds are much larger than the others (Fig. 23 *A*).

The inflorescence is terminal and racemiform. It passes the winter with its flowers well developed and protected by scale-leaves (Fig. 23 *B*); at the base of the terminal bud which encloses the inflorescence, from three to four sterile, true scale-leaves occur, then from two to three scale-leaves of a greener colour subtending vegetative buds, which are more vigorous the higher they occur on the shoot, and which have at their bases less well-developed foliage-leaves, not scale-leaves like those on the purely vegetative buds. On the fruit-bearing shoots these buds have developed into long shoots. When two vigorous shoots develop below the inflorescence the branching becomes dichotomous: if only the upper lateral shoot develops vigorously a sympodium is formed. After the above-mentioned scale-leaves three to five others (bracts) occur subtending flowers. Therefore foliage-leaves do not occur on the terminal flower-bearing shoot of the year, which may be distinguished as a terminal short shoot.

The scale-leaves of the floral shoots have hollows within the leaves similar to those which occur in the foliage-leaves, but even larger, so that the two lamellæ often arch away from each other considerably. Whether this increases their power of protecting the flower-buds and young shoots against cold and evaporation, still remains to be proved: it seems probable.

Lateral shoots are also developed on those shoots which do not bear flowers, especially in their upper part: but generally they are not so vigorous as the long shoots developed from the terminal, flower-bearing short shoot, the upper ones alone excepted which are situated immediately below the latter.

The flowers have no bracteoles.

The flowers as we have seen are fairly large even in the summer previous to the year in which they open, but are almost completely hidden by decaying leaves. The inflorescence is drooping and the throats of the corollas are turned downwards.

The corolla is urceolate, white or whitish-green (Fig. 24); its length is 5 to 6 mm.; and its breadth at the base 5 mm.;

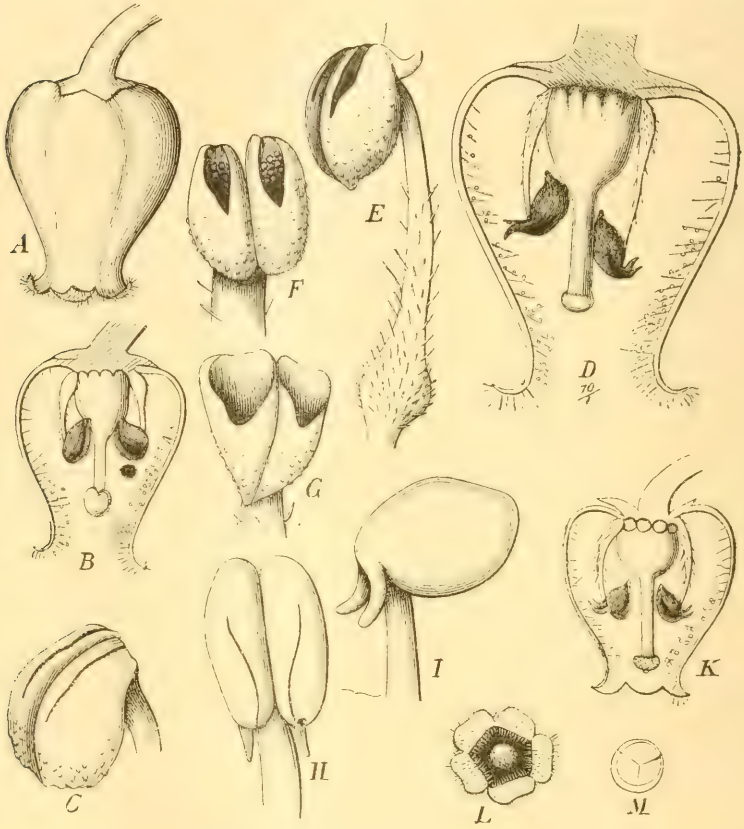

Fig. 24. *Arctostaphylos alpina.*

A, B, A flower seen from the outside and in longitudinal section; the pollen has already fallen out of the anthers though they have but just opened (5/1). *C,* An anther of the flower in question; the appendages absent. *D,* Longitudinal section through a flower with rather short style; pollen grains adhere to the hairs of the inner surface of the corolla (as in *B* and *K*). *E, F, G,* Anthers and stamens in different positions and of different ages (20/1). *H, I,* The anthers from a bud (20/1). *K,* Longitudinal section through a flower with long style. *L,* The limb and the throat of the flower seen from above; in the throat the stigma may be seen (breadth of limb about 2½ mm.; width of throat 1 mm.). *M,* pollen tetrad. (E. W., 1886.)

at the limb 2·5 to 3 mm.; the width of its throat is 1 mm. The interior of the corolla is covered with erect hairs extending as far as to the margin of the limb (Fig. 24 *D*, *B*, *K*). The

stamens stand close to the pistil; they reach about half way up the corolla or somewhat higher. Just above their slender bases the filaments suddenly grow very thick and then gradually thinner again (Fig. 24 *E*); they are covered with short, stiff hairs, and on the swollen part with small pointed warts. The anthers are dark crimson; at first they are horizontal so that the small, terminal, hornlike appendages turn directly outwards or somewhat downwards (Fig. 24 *H*, *I*); afterwards they are tilted up, so that the appendages are turned rather more upwards. Finally they open by a very wide pore which turns inwards and upwards (Fig. 24 *E*, *F*, *G*). The appendages are short, thick and glabrous, or almost so (Fig. 24 *D*, *E*, *H*, *I*, *K*); sometimes they are totally absent (Fig. 24 *B*, *C*).

The pistil is green and glabrous (Fig. 24 *D*), and the base appears to secrete honey[1] (Fig. 24 *D*).

The stigma has low antisepalous protuberances; it is situated at somewhat varying levels (Fig. 24 *D*, *K*).

The flowers are homogamous, or perhaps they begin by being protogynous for a very short time. The stigma is viscid, even in the bud, and can retain the pollen-grains (Fig. 24 *M*). But the anthers open either simultaneously with the corolla, or after the latter has expanded.

Self-pollination may very easily take place and appears to do so regularly and very early. It is facilitated by the pores of the anthers being very wide and by the large stigma taking up so much space inside the throat of the corolla, beneath the anthers, that the pollen must almost inevitably fall upon it (compare Fig. 24 *B*, *K*).

If insects visit the plant, cross-pollination may take place, the stigma being the part first touched; but the flowers open so very early in spring and in such winterly surroundings, that

[1] Skottsberg is of opinion that it is the base of the corolla which secretes honey; he mentions "10 Gruben in Grunde der Krone, halbdurchsichtig."

few insects can be astir; and those we may assume will be humble-bees (in Lappmark *Bombus lapponicus* Fabr. and *B. nivalis* Dhlb.; Poppius). Also, the flowers are so well hidden by branches and leaves that they can scarcely be seen. Therefore, the visit of insects cannot be regarded as playing any prominent part in pollination. This may be correlated with the fact that the appendages of the anthers are so unusually small, or even entirely absent; they appear to be a diminishing structure on the point of becoming rudimentary. The fact that the pores of the anthers are larger than in the other Ericaceæ also suggests self-pollination, for the pollen may be shed very easily (Fig. 24 *F*, *G*); even in quite young flowers I have found the anthers completely emptied of their contents, and pollen-grains occur in quantities all over the corolla, adhering to its hairs, which are denser than in *A. Uva-ursi* and reach as far as to the margin of the corolla (Fig. 24 *B*, *D*, *K*, *L*). The function of the hairs appears to be especially that of retaining the pollen-grains so that they may fall upon the stigma when opportunity offers. The narrowness of the throat is another contributory feature which tends to ensure self-pollination. I have hardly ever examined any open flower without finding pollen upon its stigma, and as a natural consequence of this, fruit is abundantly produced.

A. alpina appears therefore to be particularly adapted to self-pollination, while *A. Uva-ursi* — by the brighter colour and greater conspicuousness of its corolla, by the more scattered hairs in the interior of the same, and by the roughness and length of the appendages of its anthers — appears to be better adapted to cross-pollination by insects.

The drupes are spherical, black, and about 1 cm. in diameter. In the north of Scandinavia they ripen as early as August. According to Haglund and Ekstam the seeds are dispersed by frugivorous birds.

Arctostaphylos Uva-ursi (L.) Spr.

Warming, 1884, p. 46; 1885, p. 169; 1886 a, p. 18. Lindman, 1887 a, p. 70. H. Jonsson, Botan. Tidsskrift, 1895, p. 288. Poppius, 1903, p. 43. Sylvén, 1906, I, p. 129.

H. Müller, 1881, p. 385, fig. 155. Schröter, Pflanzenleben, 1904, pp. 152—157.

Material from Greenland, Iceland and the extreme north of Scandinavia.

A prostrate, creeping dwarf shrub; the out-spread and prostrate branches all occur above ground, but often in the

Fig. 25. *Arctostaphylos Uva-ursi.*

A, *B*, *F*, *G*, *H* From Denmark; *C* from West Greenland; *D*, *E* from Iceland. *A*, Shews the relative position of the buds and of the leaves. *B*, An inflorescence (July 21). *C*, Flowering branch (almost natural size). *D*, A young inflorescence, and a vegetative bud. *E*, A flowering branch with buds in the act of expanding (June 23); *HK*, the primary bud; *1* to *5*, the leaves. *F*, A seedling (1/1) with cotyledon (*G*) and primary leaf (*H*). (E. W.)

course of time the older ones become covered with soil and plant-remains. The last of the year's shoots curve slightly upwards, but afterwards become more horizontal (plagiotropic). The plant has a centrifugal growth. The younger branches are only sparingly furnished with adventitious roots; but these are more abundant upon the older ones especially those covered with soil, and one plant may break up into a number of independent plants. The leaves are more or less vertical (Fig. 25 *A*, *C*, *E*), and remain green upon the stems from two to three years.

The terminal buds on the branches were very small in July; they are protected by the basal part of the uppermost foliage-leaves. The lateral buds are also protected by the erect basal part of the petioles (Fig. 25 *A*, *B*). The buds bear scale-leaves, greenish or reddish in colour which merge by easy stages into foliage-leaves (Fig. 25 *E*). In spring the terminal buds are the first to develop, and then the axillary buds in succession from above downwards, but this succession is not always strictly observed. The lowermost buds on the year's shoots may remain dormant for several years, and may then develop. The inflorescence is terminal. When it has completed its growth a strong lateral shoot is given off immediately below it (Fig. 25 *E*), often forming a sympodium with the parent shoot.

The inflorescence is a many-flowered raceme and is formed during the year previous to that in which it opens; it passes the winter naked with its flower-buds well-developed (the specimen shown in Fig. 25 *B* is from Denmark in the month of July). It is drooping (Fig. 25 *B*, *C*), and has no foliage-leaves, only subtending scale-leaves, and two bracts at the base of each flower-stalk.

The corolla, which turns its throat downwards, is more brightly coloured and more conspicuous than in *A. alpina*: whitish with a tinge of red, the limb of a deeper red. It varies somewhat in size (from 4 to 6·5 mm. in length; the limb from 3 to 3·5 mm. in breadth; throat from 1·25 to 1·75 mm. in width). The throat is wider than in *A. alpina*. The interior of the corolla is covered with small, stiff hairs to which the pollen-tetrads (Fig. 26 *G*) adhere for a long time (Fig. 26 *L*). The hairs do not extend so far towards the margin as in *A. alpina*.

The stamens are half as long as the pistil (Fig. 26). The two appendages which proceed from the anthers extend first in a straight line and then curve upwards; they are rough with small prickly hairs (Fig. 26 *H*, *N*). Lindman found specimens in

Norway with much shorter appendages than have those found by H. Müller in the Alps and by myself in Greenland.

The bases of the filaments are slender and crowded in between the nectary and the thick base of the corolla (Fig. 26 *A*). Their form and hairiness is shewn in figure 26 *H*, *N*, etc. Besides the long hairs, small papillæ also occur.

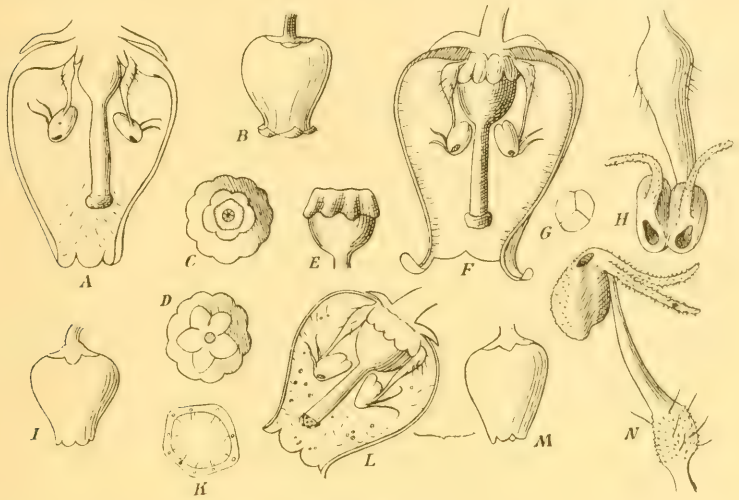

Fig. 26. *Arctostaphylos Uva-ursi.*

A—H, From West Greenland, near Holstensborg; *I—N*, from Finmark (Sakkabani, 375 m. above the level of the sea). *A*, The flower is beginning to open, the greater part of the pollen has been already shed; pollen is lying upon the stigma. *B*, Flower (about $^2/_1$). *C*, The corolla seen in front view, shewing the stigma inside the throat. *D*, The calyx and the corolla seen from below. *E*, The base of the ovary. *F*, A flower in longitudinal section (about 4 1/2). *G*, Pollen tetrad. *H*, Stamen. *I*, Even in such a bud the anthers are open and have shed their pollen. *K*, Transverse section of corolla shewing that the hairs usually occur in ten longitudinal rows. *L*, *M*, The same flower; the pollen is shed and is lying on the hairs of the corolla and in the mucilage upon the stigma. *N*, Stamen. (E. W.)

In some cases the filaments were not as hairy as were those figured by H. Müller and by Lindman or as were my specimens from the west of Finmark.

Honey is secreted by the ten-lobed disk at the base of the ovary (Fig. 26 *F*, *L*).

The flower is probably at first protandrous for a short time and then homogamous (according to Poppius homogamous in Lap-

mark). Self-pollination may take place by the pollen falling upon the stigma beneath the anthers. Even in the bud, before the corolla opens the anthers dehisce and shed their pollen. In the newly expanded flower shewn in Fig. 26 *A* the greater part of the pollen had been already shed, and pollen-tetrads were lying upon the stigma. Self-pollination is also assumed by Lindman (Central Norway). Cross-pollination by insects may easily take place. Any insect which visits the flower must touch the appendages of the anthers and shed the pollen and become dusted with it; and as the stigma is placed just at the entrance of the mouth of the corolla (Fig. 26 *F*, *L*) the insect will inevitably knock against it as well.

The visiting insects observed on the Dovre were:- *Bombus alpinus*, *B. agrorum*, and *Thrips* (Lindman).

The plant produces abundant fruit (red drupes) in West Greenland, where they may keep fresh throughout the winter. A seedling plant (from Denmark) is shewn in Fig. 25 *G*, *F*, *H*.

Vaccinium Myrtillus L.

Warming, 1884, p. 76, fig. 18. Lindman, 1887, 69, tab. IV, fig. 38. Ekstam, 1894, p. 427. Skottsberg, 1901, pp. 11, 13. Poppius, 1903, p. 42. Sylvén, 1906, I, p. 127.

H. Müller, 1873, p. 355, fig. 133; 1881, p. 381. Schröter, 1904, pp. 166, 176—78, tab. IX.

A dwarf shrub with erect, assimilatory shoots, and long, subterranean runners which have elongated internodes, bear scale-leaves, and have a straight apex (Fig. 27 *A*, *B*). Roots, hair-like and branching, spring from the axils of leaves, above the axillary buds (Fig. 27 *A*); some of the roots become thicker. In course of time the runners, which branch, become woody and as thick as goose-quills, and form annual rings. They may live for more than a year beneath the surface of the soil, before they bend upwards and develop into an assimilatory leaf-bearing shoot (Fig. 27 *C*). While the sub-

terranean runner is round, the assimilatory shoot is angular owing to the edges of the decurrent leaves (Fig. 27 *C*). The year's shoots are unbranched; they have scale-leaves at their bases. It is a usual thing for the terminal bud to die and then the apex of the shoot has the form of a small, pointed cone (Fig. 28 *L*; Fig. 27 *C*). The uppermost lateral bud generally continues the growth sympodially. Besides this bud, from one to three of the other upper lateral buds may grow out. The foliage-leaves fall in autumn. The buds are protected by scale-leaves which sometimes persist at the base of the year's shoot even after the leaves have come out.

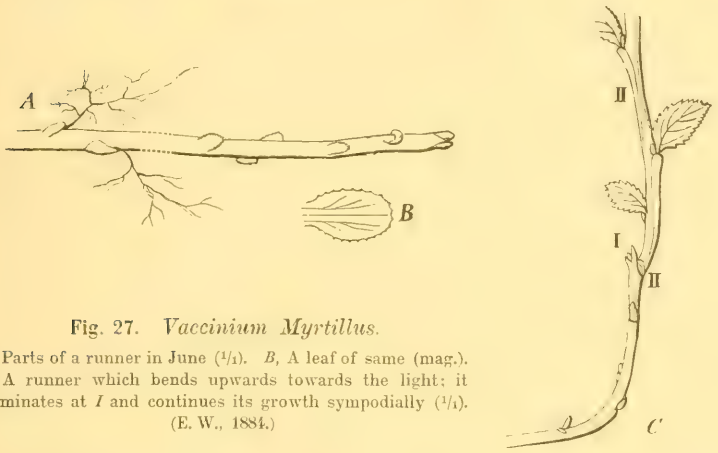

Fig. 27. *Vaccinium Myrtillus.*

A, Parts of a runner in June (1/1). *B*, A leaf of same (mag.). *C*, A runner which bends upwards towards the light; it terminates at *I* and continues its growth sympodially (1/1). (E. W., 1884.)

The flowers occur singly in the axils of one or two of the lower foliage-leaves on the year's shoot, but rarely in the axil of the uppermost scale-leaf. They are 4- and 5-merous.

The corolla is urceolate-globose (Fig. 28), and entirely glabrous. Usually it is of a dull deep-red colour, but according to Lindman and Skottsberg on the Dovre and in Lapland the colour is much deeper than in the lowlands. The length is from 4 to 5 mm., the width of the throat is 2 mm.

The filaments are bent inwards towards the style, and the anthers stand erect, parallel to the latter (Fig. 28 *B*). The pores

at the apex of the two tubes into which the anthers are prolonged lie immediately below the stigma which protrudes somewhat further. The pale brown anthers are slightly rough (Fig. 28 *E*, *F*); on their dorsal side they have moreover two upwardly curving rough appendages which stand at about the middle of the corolla.

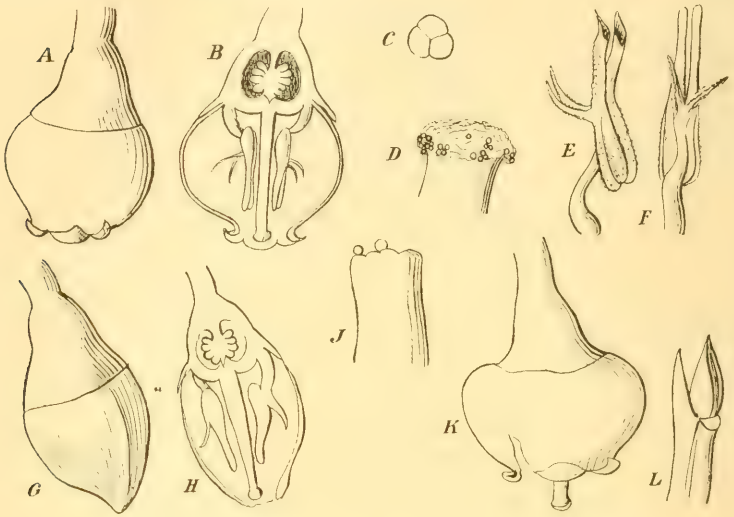

Fig. 28. *Vaccinium Myrtillus.* — (From Finmark).

A, Open flower. *B*, Longitudinal section through flower; there are already many pollen tetrads (*C*) upon the stigma (*D*). *E*, *F*, Anthers of *B*. *G*, *H*, In this bud the anthers are open, and the pollen falls easily out of them when they are dry, but pollen has not yet been shed upon the stigma; on the latter two small drops (*J*) have been secreted. *K*, A flower the corolla of which has been split by insects (Stockholm). *L*, Apical portion of a branch with the uppermost lateral bud; to the right the scar left by the subtending leaf. (E. W.)

The flower is protandrous for a very short time and then homogamous (this agrees with the statement of Lindman, Ekstam and H. Müller; according to Alli the plant is slightly protogynous). The anthers open while still in the bud (Fig. 28 *G*, *H*), and the pollen falls easily out of them as soon as they are dry. At any rate the stigma ripens immediately after the flower has expanded, but even in the bud I have seen drops secreted upon it (Fig. 28 *J*).

Pollen tetrads (Fig. 28 *C*) may be found scattered abundantly upon the style, and may also, though with great difficulty, find their way to the small stigma (Fig. 28 *D*) which is situated at, or immediately within, the throat of the corolla, sometimes however slightly beyond the latter.

Honey is secreted abundantly and occurs in large drops on the disk.

On the Dovre the flowers are visited by *Bombus alpinus* (Lindman), in Lapland by *B. consobrinus*, *B. lapponicus* and *B. scrimshiranus* (Skottsberg).

The flowers are often found split at the throat; they have been split by insects (Fig. 28 *K*); and then the style is thrust far out.

The form of the ovary varies (see figures, and Sprengel, Entdeckter Geheimnis, tab. XXII, fig. 21. H. Müller, Befruchtung, fig. 133, 1; Lindman l. c.).

Vaccinium uliginosum L.

et var. **microphyllum** Lange (l. c. p. 91).

Kjellman, Fr., 1883, p. 508 with fig. Warming, 1884, p. 77; 1885, p. 197, fig. 16; p. 206. 1886b, p. 118. Lindman, 1887, p. 68. tab. III, fig. 35. Ekstam, 1894, p. 427. Poppius, 1903, p. 42. Skottsberg, 1901, pp. 11, 15. Sylvén, 1906, I, p. 128.

H. Müller, 1873, p. 355; 1881, p. 381. Schröter, 1904, pp. 172—74.

Material from Greenland, Iceland and Finmark.

A dwarf bush with subterranean runners the apices of which are straight (Fig. 29 *D*); at the point where the runner rises above the soil in a curve, the scale-leaves merge by easy stages into foliage-leaves (Fig. 29 *C*).

Very slender roots, which branch rather abundantly, arise from the leaf-axils above the axillary bud (Fig. 29 *E*).

The foliage-leaves generally fall at the end of the season of growth, often turning red, but they may persist in a decaying and

colourless condition. They are covered on both sides with a glaucous layer of wax which prevents them from getting wetted; the rain-drops therefore can be seen sparkling with a silvery lustre on them.

The buds are protected by closely fitting scale-leaves (Fig. 29 *A*). The terminal bud usually fails to develop, and at the end of the shoot the small, conical, decaying portion of it may be observed (Fig. 29 *G*, *F*); sometimes a larger part dies than merely the terminal bud. Below the dead portion two to

Fig. 29. *Vaccinium uliginosum*. (From West Greenland.)

A, Branch in spring (Disko; June 2, 1907: Porsild). *B*, To shew the mode of branching (reduced); *I*, *II*, *III* are successive axes. *C*, Runner with scale-leaves which merge by easy stages into foliage-leaves (slightly mag.). *D*, Apex of a subterranean runner. *E*, A runner with branches and roots in its leaf-axils (July). *F*, Portion of a branch, shewing the position of the leaf relative to the axillary bud and the dead apex of the shoot (*I*). *G*, Branch (from Upernivik); the snow has recently disappeared (May 17, 1887); *I* is the apex of the main axis; the terminal bud is floral. (E. W.)

four axillary buds develop into new shoots so that the branching becomes dichotomous (Fig. 29 *B*). The lower part of the year's shoot remains unbranched.

At the end of the flower-bearing branches one to four buds occur which develop into dwarf-shoots, each bearing from one to two flowers (Fig. 30 *A*, *C*, *E*); the buds are protected by scale-leaves.

The flowers are formed during the year previous to that

in which they open (Fig. 30 *G*, *H*); 4- and 5-merous flowers are found on the same plant, but other numbers also may occur. The corolla is tinged with rose-colour or else is white (Skottsberg:- "der nach aussen gewandte Teil der Krone purpurroth in Lapland"). I found the flower to be scentless in Greenland, but according to Wormskjold it has "a pleasant, sweet, aromatic perfume which almost recalls that of the Woodruff (*Asperula odorata*)." Lindman found that the specimens on the Dovre mountain had a strongly pungent, spicy fragrance.

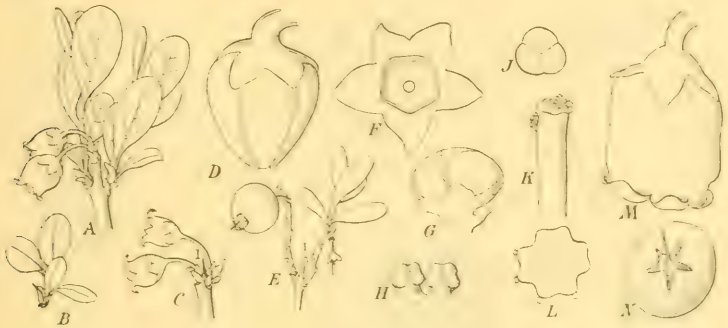

Fig. 30. *Vaccinium uliginosum*. (From West Greenland.)

A, Branch (Upernivik: July 13, 1887); slightly mag. *B*, Shoot in the act of expanding (Upernivik; July 10): the largest leaf is 6 mm. long. *C*, Apex of a branch bearing two flowers (Upernivik: July 10); the corolla 3 mm. in length. *D*, Flower-bud of *V. uliginosum* f. *microphylla*; the anthers are open, and the pollen is lying loose in them. Upon the stigma a small drop of mucilage is seen, but no pollen (June). *E*, A fruit-bearing branch (Ivigtut; Aug. 20) reduced; *I*, Main axis. *F*, 5-merous calyx of a flower with 4-merous corolla, 8 stamens, and an 8-lobed nectary. *G*, A flower-bud (from Fig. 29 *G*). *H*, Stamens of the same. *J*, Pollen tetrad. *K*, In the mucilage upon the stigma occur many pollen grains; from the flower *C* in Fig. 31 (Godthaab; June 29). *L*, The nectary, with drops of honey. *M*, Flower of f. *microphylla*; length 6 mm. *N*, Ripe fruit. (E. W.)

The corolla is urceolate-globose and drooping (Fig. 30 *A*, *C*); on looking down into the flowers, in some, only the stigma and the scabrous anthers (Fig. 31 *F*, *G*) with their appendages are visible (Fig. 31 *D*), in others, a greater part of the interior (Fig. 31 *B*). The corolla is from 3·5 to 6 mm. long, in the Scandinavian specimens it measures as much as 7 to 8 mm. in length; the throat is from 3 to 4 mm. wide.

The flower is slightly protandrous (as in the Alps according

to H. Müller, Befr., p. 355); the anthers are open and the pollen lies loose in them before the corolla has expanded (Fig. 30 *D*) and before the stigma is quite ripe. Homogamy ensues and lasts for a longer time (according to Lindman and Ekstam "the flower is protogynous-homogamous").

The filaments bend inwards and the anthers touch the style (Fig. 31 *C*). In a smaller form with an ovoid corolla Lindman found the stigma wide spreading.

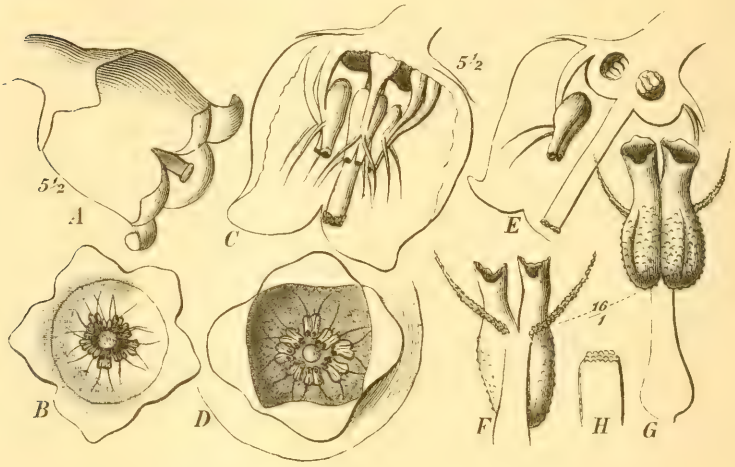

Fig. 31. *Vaccinium uliginosum* L. f. *microphyllum* Lange.

A, Open, 5-merous flower from West Greenland (June 29, 1884). *B*, Same seen from above. *C*, A 4-merous flower of the same date; there is pollen in the anthers, and the stigma is able to retain the pollen. *D*, The same seen from above. *E*, Of same date. *F*, *G*, Stamens of the same. *H*, Apex of the style. (E. W., 1885.)

The stigma is placed just within or at the throat of the corolla, but it scarcely projects beyond it. The anthers stand at a slightly lower level with their appendages spreading straight outwards or directed upwards (in the inverted flower downwards; Fig. 31 *C*). Consequently the flowers are distinctly adapted for cross-pollination. An insect in search of honey (Fig. 30 *L*) cannot avoid touching the appendages with its proboscis and thereby shedding the pollen. The following insect-visitors have been observed: *Bombus nivalis* on the Dovre (Lindman); *Bombus consobrinus*,

B. lapponicus and *B. scrimschiranus* in the north of Sweden (Skottsberg).

But self-pollination also must easily take place as the flowers are drooping and the stigma consequently is below the anthers. That self-pollination takes place I conclude from the fact that in one of the districts of Greenland (Godthaab), where it was still quite winterly and quantities of snow were lying on the ground, pollination had already taken place, although I never observed any insects visit the flower, either there or anywhere else in Greenland.

The flowering period is very long; during the whole of the summer I spent in Greenland I found newly expanded flowers.

Abundant fruit is set regularly in East and West Greenland and ripens the same year as that in which the plant flowers. The berry is globular, from 9 to 12 mm. in diameter.

Vaccinium Vitis-idæa L.

et f. **pumilum** Hornem. (Lange l. c. p. 90).

Kjellman, 1883, p. 508, fig. Warming, 1884, p. 77; 1885, p. 194, figs. 14, 15; p. 205; 1886 b, p. 7. Lindman, 1887, p. 69. Ekstam, 1894, p. 427; 1897, p. 124. Poppius, 1903, p. 42. Sylvén, 1906, I, p. 128, tab. IX.

H. Müller, 1881, p. 380, fig. 153. Schröter, Pflanzenleben, pp. 163—172.

Observations and material from Greenland, Norway (Finmark) and Sweden.

A dwarf shrub with long, subterranean runners, which bear scale-leaves (Fig. 32) and live sometimes for more than a year beneath the surface of the soil, being seen to consist of older parts which are brown, and younger parts pale in colour. The runners have very slender, branching roots which are given off beyond the buds, from the axils of leaves (Fig. 34 *F*); they have a straight apex (Fig. 32).

The aerial shoots are a few centimetres high; consequently, they are often hidden by moss and other plants; they have coriaceous foliage-leaves which remain green a couple of years or more.

The buds are protected by scale-leaves, hence the limits of each year's growth are distinctly marked.

The flowers pass the winter in terminal buds protected by scale-leaves. They occur from two to four (or several), in a racemiform cluster; each has two bracteoles a little above the base of the pedicel; 4- and 5-merous flowers may be found in the same inflorescence. They always turn the mouth of their pale-rose-coloured, campanulate corolla down-

Fig. 32. *Vaccinium Vitis-idæa* L., f. *pumilum*. (From West Greenland (Christianshaab), July 26, 1884.)
A, Small plant with its runners. *B*, A leaf. (E. W., 1885.)

wards (Figs. 33, 34) and are inconspicuous and more or less hidden by leaves; they are scentless. The flowers of the typical form from Central Europe are from 8 to 10 mm. long, and the throat is from 7 to 8 mm. wide, but the flower of the form *pumilum* is always smaller (5 to 8 mm., with the throat 5 mm. in diameter; in Nova Zembla according to Ekstam 4 to 8 mm.); compare my figure with that of H. Müller; both are magnified 5 times.

In the typical form the style projects far beyond the corolla, and the pores of the anthers are widely separated from the stigma (Fig. 33 *H*; Fig. 34 *B*); in the Greenland form *pumilum* the distance between the pores and the stigma is less, one

reason being that the flowers are smaller in size; but they also differ somewhat in other details of structure. In some the relation of the different parts to each other is the same as in the typical form (Fig. 33 *A*, *B*); but in others the pores of the anthers are situated almost exactly in the throat and therefore much nearer to the stigma, which is situated only slightly beyond the throat or practically in it (Fig. 33 *C*, *D*). Lindman also mentions differences in the flower, and on Dovre he has observed this form with a flower 7 mm. long, and the anthers protruding and standing rather close to the stigma. Lastly

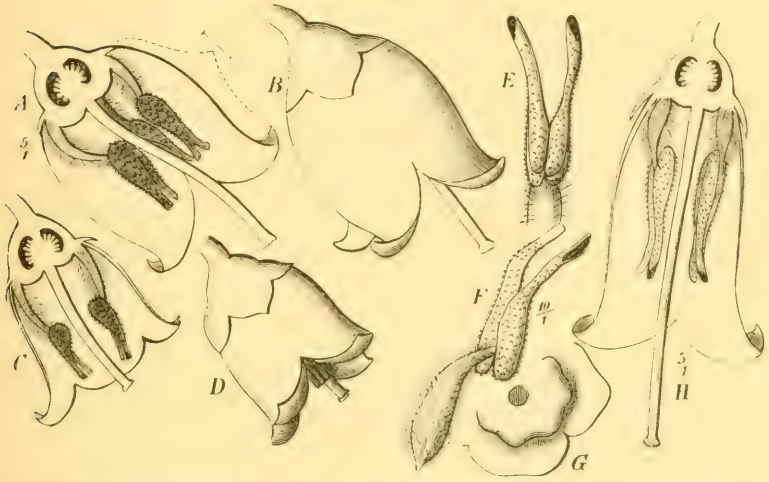

Fig. 33. *Vaccinium Vitis-idæa*. *A*—*G*, forma *pumilum* from West Greenland (Christianshaab; July 26, 1884). *H*, from Stockholm: typical form. *A*, *B*, One of the larger flowers. *C*, *D*, One of the smaller flowers. *E*, *F*, Stamens of *A*. *G*, The nectary. *H*, A flower magnified as *A*—*D*; June 17, 1881 (Cf. Fig. 34 *A*). (E. W., 1885.)

it may be mentioned that there are even some cases in which the stigma stands somewhat lower than the pores (Fig. 34 *D*).

These differences no doubt depend partly upon the growth of the style, but only partly. Ekstam writes: — "der Griffel wächst später noch so dass die Narbe in einer völlig erblühten Blume an den Blütenrand heranragt oder sich ein wenig über diesen erstreckt."

In other respects I see no difference between the European form and the Arctic form *pumilum*[1].

The filaments in both the forms are covered with long, rough hairs (Fig. 33 *F*, *A* etc.; Fig. 34 *E*) which perhaps serve to retain the honey, but most probably are a substitute for the appendages which occur on the anthers in *V. uliginosum*.

The anthers lie close to the style and are rough with small pointed protuberances (Fig. 33 *E*, *F*) which doubtless cause the insects to touch the anthers more violently and thus increase the resulting shock.

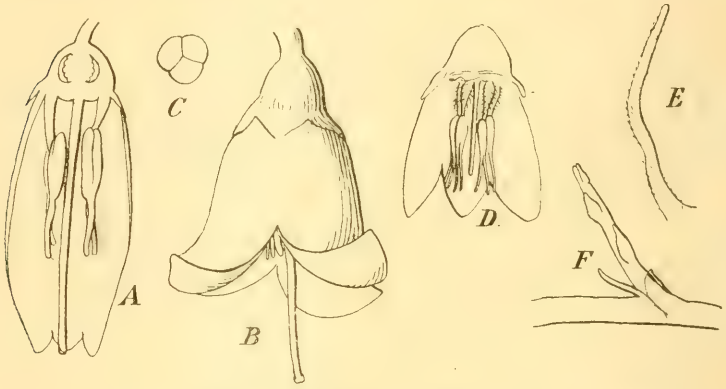

Fig. 34. *Vaccinium Vitis-idæa.*

A, Flower-bud (Stockholm); length 9 mm. *B*, Open flower (Finmark; July 15, 1885); length 8 mm. from the stalk to the mouth of the corolla. *C*, Pollen tetrad. *D*, Flower (from West Greenland, Auleitsivik Fjord); only a few pollen tetrads are left in the anthers. *E*, Hair from the filament. *F*, Portion of a runner with a branch and a root in the axil of a scale-leaf. (E. W.)

Slight protandry occurs (H. Müller, p. 38, records homogamy; Ekstam reports homogamy or slight protandry in Nova Zembla). I have found the pores of the anthers open a long time before the flowers expand, consequently, the pollen may fall out immediately the flowers open.

Self-pollination appears to be able to take place, owing to

[1] Ekstam writes, l. c. p. 427: "der Stempel ist in der Knospe hakenformig gebogen; beim Eröffnen der Blüthe richtet er sich doch nicht ganz auf." This I have not observed.

the position of the pores, and may occur more easily in *pumilum* than in the form from Central Europe; but the Greenland flower is evidently adapted also for pollination by insects. Honey is secreted by the thick, lobed disk at the base of the style (Fig. 33 *G*). The style and the stamens are often placed near to the upper side of the corolla. Lindman has seen specimens in which the stamens had been bitten off by insects (Dovre). Ekstam and O. Santesson saw *Bombus* visit the flower.

The plant sets fruit in West Greenland (Ekstam records: — "Epizoische Samenverbreitung" "durch beerenfressende Vögel" in Nova Zembla).

Vaccinium Oxycoccos L.

et var. **microcarpum.** *Oxycoccos palustris* Pers. et f. *pusillus* Rupr., *O. microcarpus* Turcz.

Warming, 1884, p. 49. Lindman, 1887, p. 73. Poppius, 1903, p. 42.

Observations from Norway (Finmark) and Denmark.

A creeping dwarf shrub; the prostrate, rooting stems which occur above ground, are very slender and delicate, and have elongated internodes (Fig. 35); the roots, which arise from above the axillary buds, are hair-like and branch fairly abundantly (Fig. 35 *K*).

The foliage-leaves remain green on the stems about two years; their under sides are covered with a very glaucous layer of wax.

The buds are protected by scale-leaves, and the lateral buds also by the somewhat erect, subtending petioles (Fig. 35 *F*, *G*, *H*). Branches arise not only below the apex of the floral shoot (Fig. 35 *B*, *D*, *E*), but also occur scattered here and there lower down on the stem. The year's growths have at their bases a few scale-leaves which are not close-set.

The flowers are in a small inflorescence of from one to four flowers, at the apex of the leaf-bearing shoot. They are

formed during the year previous to that in which they open (this is also the case in Denmark). The flowers pass the winter in an almost globular bud, which is much larger than the more ovoid leaf-buds (compare Fig. 35 *A* and *J* with *H*). The flowers, which have long, slender peduncles are lateral and situated in the axils of scale-leaves (umbellate); the floral shoot terminates blindly above the flowers where it bears barren scale-leaves (Fig. 35 *B*); but sometimes it keeps on

Fig. 35. *Vaccinium Oxycoccos.* (From Denmark).

A, A branch (slightly mag.); March 8; the terminal bud is floral. *B*, *C*, Two branches bearing fruit — the flowering stage at least, being over (slightly reduced); I, axis of the first order; II, axis of the second order. *D*, *E*, The basal portion of *I* has borne flowers and is now dead (March 25); below that, new branches occur more or less sympodially. *F*, *G*, Shewing the position of the buds as subtended by the erect petioles. *H*, A branch entirely vegetative (Oct. 28). *J*, A branch with terminal floral bud (Oct. 28). *K*, Portion of a stem shewing the position of the axillary bud (*g*) and of the root (*r*) in relation to the leaf (*f*); Oct. 20. (E. W.)

growing and develops into a leaf-bearing shoot (Fig. 35 *C*). It may appear as if there were a terminal flower, but this can hardly be the case. Sometimes one of the upper foliage-leaves subtends a lateral, entirely floral shoot. After flowering, one or several of the upper buds may develop into new shoots and then sympodial or dichotomous branching occurs (Fig. 35 *D*, *E*).

Each flower has two bracteoles half way up its stalk.

The flowers are protandrous; even in the bud (Finmark)

the pores of the anthers are open and the pollen-tetrads fall out easily (Fig. 36 *B*). The four petals of the deep-rose-red corolla are quite free, and in the expanded flower they are bent back (Fig. 36 *A*). The length of the petals is from 6 to 7 mm.; and that of the stamens from 4 to 6 mm. The filaments have fine hairs at their edges; the anthers are covered with small warts (Fig. 36 *E*, *F*); they dehisce even in the bud, and before the stigma is ripe, by means of two pores, one at the

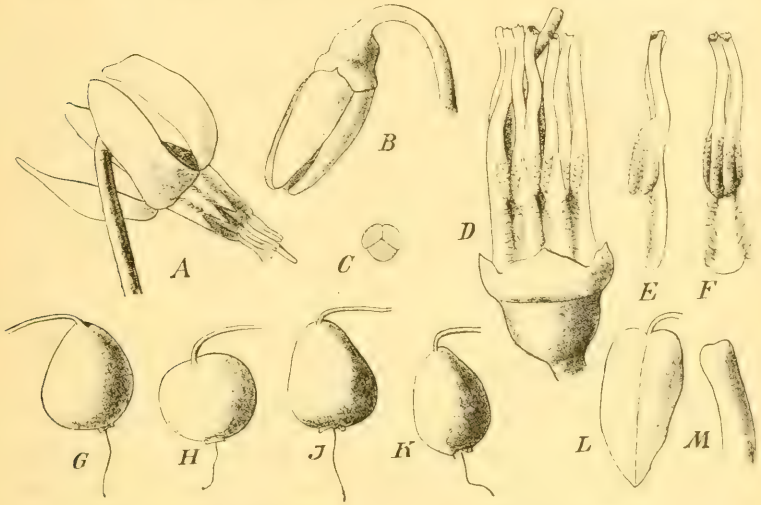

Fig. 36. *Vaccinium Oxycoccos.* (From Finmark, Norway.)

A, The anthers contain a quantity of pollen (magnified as *A* in Fig. 37). *B*, A flower-bud; the pollen lies loose in the anthers, but has not yet fallen out of them. *C*, Pollen tetrad. *D*, *E*, *F*, Androecium and stamens of *B*. *G*, *H*, *J*, *K*, Fruits of var. *microcarpum* (from Bosekop in Finmark). *L*, Leaf of same, length 5 mm. *M*, Style with stigma of *B*. (E. W.)

apex of each of the two long, non-coherent tubes into which they are prolonged.

In the expanded flower the stamens are erect and stand close to the pistil (Fig. 36 *A*; Fig. 37 *A*), which is at first only slightly longer, but gradually increases. The pollen tetrads (Fig. 36 *C*) are easily shed.

At the base of the style there is a disk which secretes honey (Fig. 37 *B*).

Lindman speaks of self-pollination as rather uncertain, because the stigma is so far removed from the anthers; but in the Greenland specimens it is closer to them than in the specimens from temperate Europe; in Danish specimens the style grows to a length of from 7 to 8 mm., and may project from 1·5 to 3 mm. beyond the anthers (Fig. 37). In Finmark I found the length of the style to be from 5·5 to 6 mm., and it projected only from 0·5 to 1 mm. beyond the anthers (Fig. 36 *A*).

Fig. 37. *Vaccinium Oxycoccos.* (From Denmark.)
A, A large flower; length of stamens 6 mm.; that of the petals 6½ mm. *B*, Nectary. (E. W.)

The fruit varies as regards its form as shewn in Fig. 36 *G—K*.

The var. *microcarpum* with downy pedicels has not yet been found in Greenland, but the specimens which occur there may have as small leaves as *microcarpum*. In Bosekop (Finmark) the two forms were found growing together. The flowers of the one plant are not quite twice as large as those of the other.

Fam. *Pirolaceæ*.

Pirola rotundifolia L. et var. **grandiflora** Raddi.

Warming, 1884, pp. 75, 97; 1885, p. 165, fig. 2; 1886, b, pp. 7, 18. Lindman, 1887, p. 74. Ekstam, 1897, p. 123. Abromeit, 1899, p. 40. Poppius, 1903, p. 44. Sylvén, 1906, p. 134.

H. Müller, 1881, p. 376, fig. 150.

Observations and material from West and East Greenland.

An evergreen, somewhat suffrutescent plant; the long, slender, subterranean runners have long internodes and bear scale-leaves. Fig. 38 *A* shews a runner like the one in question; it is there shewn as having risen above the ground in a curve and having formed a vertical aerial shoot (*I*) with two foliage-leaves (*f*, *f*), which has died down to the ground; but from its base a new shoot (*II*) has been given off which

Fig. 38. *A—C, Pirola rotundifolia* (from Denmark), *D, P. secunda* (from Denmark).

A, A rhizome terminating in *I*, in a dead inflorescence and two decayed foliage-leaves (*f*, *f*); *II*, A lateral shoot bearing 3 foliage-leaves. *B*, A subterranean runner with branch; of the two shoots the lower one is below the surface of the soil, and the upper one has risen above the ground and bears a large terminal bud (*g*). *C*, A vertical rhizome terminating in a (dead) inflorescence; *f*, a foliage-leaf. Two pale lateral shoots bearing scale-leaves rise straight into the air and are somewhat abnormally lengthened owing to the fact that the plant has been overgrown by moss. *D*, The apex of a runner of *P. secunda*. (E. W.)

bears three foliage-leaves and terminates in a bud protected by scale-leaves. In Fig. 38 *B* a similar runner is shewn which has risen above the ground (bearing the terminal bud, *g*) and has given off a branch at *a*. The runners are curved like a hook at the apex (Fig. 39 *B*, *C*, *E*). Their roots spring from the axils of the scale-leaves, above the axillary buds (Fig. 39 *A*, *B*, *D*, *F*), and are very slender and sparingly

branched (Fig. 39 *A*, *B*). Fig. 38 *C* shews a vertical rhizome with a single foliage-leaf and terminating in an inflorescence which is now dead; it was overgrown by Sphagnum; two slender shoots bearing scale-leaves arise from it straight into the air. Fig. 40 *D* is a runner which has risen above the ground and formed an aerial part bearing a single foliage-leaf.

Each aerial year's-shoot bears some thin scale-leaves at its base besides one to three foliage-leaves (compare Fig. 40 *B* and *C*). The latter may remain green two (to four) years (Fig. 40 *A*; Fig. 41) and may afterwards remain on the branches in process of decay for a longer time before crumbling away. The aerial part of the shoot may attain an age of several years

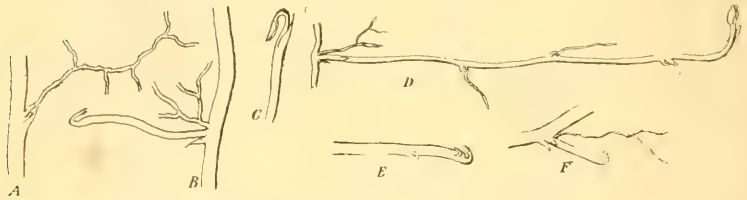

Fig. 39. *Pirola rotundifolia* var. *grandiflora*.

A—*C*, Parts of different runners, shewing the positions of the roots and branches, as also the form of the shoot-apices. *D*, *P. chlorantha* (from Denmark), the runner is rising above the ground (almost natural size). *E*, *F*, Parts of different runners. (E. W.)

before its growth is stopped by a terminal inflorescence; it then dies down to the uppermost lateral shoot (Fig. 38 *A*).

Vegetative reproduction takes place by means of the runners, hence this species often occurs in patches, forming fairly large clusters in copses and on moors; but as the runners are long and wide-spreading it nevers occurs as a dense covering.

The flowers have a faint perfume suggestive of that of the Lily of the Valley. The petals are white, tinged with rose-red especially towards the margin; the calyx and the pedicels are deep-red.

While flowering the petals are widely expanded (Fig. 42) so that the corolla is wheel-shaped, measuring from 14 to 30 mm.

in diameter (as also, according to Lindman, p. 75, do those upon the plants found on the Dovre mountain: in Nova Zembla, according to Ekstam they measure from 12 to 20 mm.; and upon *Pirola rotundifolia* in Denmark and Sweden, they measure from 14 to 16 mm.; cf. Fig. 42 *A* and *K*). The two back petals arch slightly above the erect stamens (Fig. 42 *B*).

Fig. 40. *Pirola rotundifolia* var. *grandiflora*. (From Upernivik in West Greenland; May 27.)

A (about 1/1); the basal portion of a flowering plant; the rhizome bears the leaves *a* and *b* on that year's growth which is the oldest but one; *1—5* foliage-leaves and *6—10* scale-leaves of the next year's growth; *p*, scale-leaves. *B*, The apex of a runner with two foliage-leaves (*L*) and a terminal vegetative bud. *C*, A similar runner with a terminal floral bud. *D*, A runner with branches and bearing a foliage-leaf near its apex. *E*, An inflorescence which has been taken out of a terminal floral bud. *F—I*, Parts of a flower from the same inflorescence; (*F*) stamen; (*G*) petal; (*H*) petal with two stamens; and (*I*) pistil; length of petal about 1/2 mm. (E. W., 1907.)

Homogamy appears to be the rule. Even before the flower is quite open the stigma is viscid and the pores of the anthers are widely open (Fig. 42 *H*, *I*).

In the bud the pores of the yellow anthers are turned downwards (Fig. 42 *H*, *I*) as in the other species of *Pirola*, so self-pollination is impossible, as Lindman has also pointed

out; but in the open flower the anthers are tilted backwards and the pores then face upwards (Fig. 42 *D*, *F*). In the fully open flower the pollen tetrads fall in quantities out of the anthers without hindrance.

The style is bent forwards and downwards (Fig. 42 *A*, *B*, *K*). The stigma consists of five low protuberances (which appear to be somewhat higher than those in the typical form of *P. rotundifolia*) seated upon the apex of the style which is flat and has a sharp edge (Fig. 42 *G*).

Fig. 41. *Pirola rotundifolia*.
(From Greenland, Tasuisak; Aug. 1896.)
Shoot with scale-leaves and 3 year's growths with foliage-leaves. (E. W., 1907.)

I have not observed secretion of honey in any flowers on the Greenland plants; neither has Ekstam in those from Nova Zembla nor Poppius in Finland. Cross-pollination by insects must be of possible occurrence, and indeed appears a necessity (visitors in Finland, cf. Poppius l. c.) because in the fully open flower the pores of the anthers turn upwards, away from the stigma, so that the pollen will have difficulty in falling down spontaneously upon the latter. The Greenland form *grandiflora* appears, however, to be somewhat better adapted for self-pollination than the European *Pirola rotundifolia*, because in the former the distance between the pores and the stigma is only from 3 to 5 mm., while it is 6

to 8 mm. in the latter. The style in the European *P. rotundifolia* is relatively longer and also is often more downwardly directed (cf. Fig. 42 *A—B* and *K*). In flowers from Denmark and Sweden I have found styles measuring from 7 to 8 mm. in length, while those in the Greenland flowers measured 5 to 6·5 mm. only. In addition to this the stamens appear to be

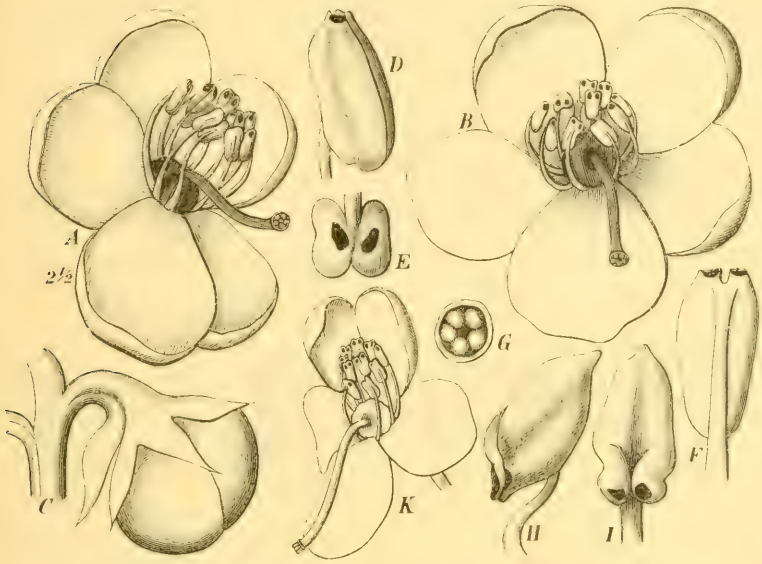

Fig. 42. *Pirola rotundifolia* L. var. *grandiflora* (*A—I* from West Greenland). *P. rotundifolia* L. (from Stockholm; July).

A, B, Flower seen in side and front view (July 26, 1884). *C*, A flower-bud (its bract reaches a little way along the flower-stalk); about $^3/_1$. *D, E, F*, The anthers of an older flower. *G*, Stigma seen from above. *H, I*, The anthers of a younger flower before they change their position; about $^{10}/_1$. *K*, A flower from Stockholm; magnified as *A* and *B*; about 15 mm. in diameter. (E. W., 1885).

more erect in the typical form of *P. rotundifolia*, but bent further forward and somewhat shorter in *grandiflora*.

The flowers are formed during the year previous to that in which they open and reach the stage of development shewn in Fig. 40 *E—I*. The floral buds are larger and more ovoid than are the purely vegetative buds (cf. Fig. 40 *B* and *C*).

Ripe capsules are developed in West Greenland, but perhaps this is a rare occurrence.

The diagram of the flower is the same as that given in Eichler, Blüthendiagramme, Vol. I, p. 344.

Pirola rotundifola L. var. *β arenaria* Koch.

Judging from herbarium material the style appears to be even shorter than that in var. *grandiflora*, and the flowers to be smaller than those of *P. rotundifolia*.

Pirola minor L.

Ekstam, 1894, p. 429. Poppius, 1903, p. 44.

In the structure of its shoot it is quite similar to *P. rotundifolia*.[1] The leaves are still of a fresh green colour on two-year-old shoots.

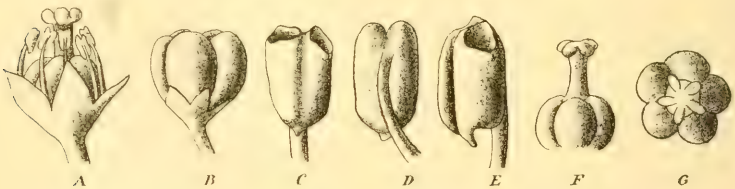

Fig. 43. *Pirola minor*. (From West Greenland, Kingua Tassiusak).
A, A flower; the petals have been removed (about 3/1). *B*, A flower (slightly mag.). *C*, *D*, *E*, Anthers. *F*, Pistil. *G*, Ovary and stigma seen from above. (E. W.).

I have only a few notes on the biology of the Greenland flowers as I did not meet with any living specimens. Fig. 43 is drawn from spirit-material.

The diameter of the flower is only from 7 to 8 mm. According to Poppius it is scentless and devoid of honey in Finland, and very rarely visited by insects. According to Axell

[1] Also *Pirola secunda* and *P. chlorantha* correspond in the structure of their shoots with *P. rotundifolia* (Fig. 38 *D*; Fig. 39 *D*); *P. umbellata* differs somewhat, its stems being lignified to a greater extent, and *P. uniflora* differs in an even higher degree.

(Sweden) it is homogamous, and according to Ekstam (Nova Zembla) protogynous-homogamous. Ekstam writes: — "In der jungen Knospe sind die Staubfäden dicht an den Stempel gedruckt, welcher bereits reif zu sein scheint. Die Antheren sind nach aussen gebogen, mit den Poren nach unten gegen die Basis. Beim Eröffnen der Blüte haben dann die Antheren einen Bogen von 90° beschrieben und wenden also die Poren nach der Öffnung der Blüte. Da indessen der Stempel gerade und länger ist als die Staubfäden, kann eine Selbstbestäubung hier nicht stattfinden (Birkenregion bei Åre)."

The plant sets ripe fruit in Greenland, at any rate in the southern districts.

Pirola uniflora L.

Warming, 1884, pp. 75, 76, 86; fig. 23. Lindman, 1887, p. 74. Ekstam, 1894, p. 429. Poppius, 1903, p. 44. Malme, G., 1907, Några bildningsafvikelser i blomman hos Pyrola uniflora L. (Svensk Botan. Tidskrift, 1, p. 270).

Observed in Finmark.

From the horizontally growing roots leaf-bearing shoots proceed at irregular intervals; they are usually unbranched, and are about 8—12 cm. in height; they terminate in a flower and reach an age of 2—4 years. At the base of each shoot a root usually arises upon the mother-root (Warming, 1884). Each shoot has therefore from 2 to 4 year's growths, each of which, after some scale-leaves, bears a rosette of 3 (2—5) foliage-leaves, and lastly the shoot terminates in a bud protected by scale-leaves which lives over the winter. The scale-leaves are thin and very distinctly veined.

The flower is white, drooping and strongly scented: it is homogamous, and is devoid of honey.

The petals are almost horizontally expanded (Fig. 44). In Finmark I found the diameter to be from 14 to 16 mm.;

Lindman (on the Dovre), 13 mm.; Ekstam, 12—20 mm.; Müller (in the Alps), 22 mm.

The stamens are spreading and parallel with the corolla; they are entirely glabrous and the pores at the apex of their two short anther-tubes (Fig. 44 *C*) turn outwards, away from the stigma, the five rays of which are large and erect and stand opposite to the diaphragms of the ovary (Fig. 44 *C*).

The stamens generally occur in groups of 2 and 3;

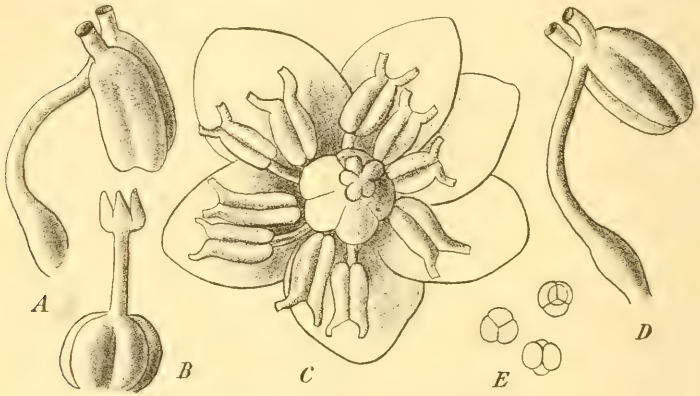

Fig. 44. *Pirola uniflora.* (Alten in Finmark; July 6, 1885).

A, Stamen. *B*, Pistil. *C*, An abnormal flower (fully $^3/_1$; 14 mm. in diameter): 6-merous calyx; 6-merous corolla; 10 stamens; 5-cleft stigma; the antisepalous stamens have the larger anthers. *D*, Stamen. *E*, Pollen tetrads. (E. W.)

Linné has, according to Lindman, given a diagram of this in his "Ölandska Resan."

Fig. 44 *C* shews one of the frequent deviations from the normal type with 6-merous calyx and corolla (see Malme, l. c.).

In Finland Poppius found it to be but rarely visited by insects (the pollen-seeking *Aricia meteorica* L.).

After having set fruit, the shoot dies away entirely, if not during the same year, then in one of the following years. The plant appears never to develop lateral shoots.

A summary
of
the morphology and biology of the *Ericineæ*.

All the Ericineæ are adapted for cross-pollination by insects, and some instances are known of the visits of insects (mostly species of humble bees) to the flowers, although these visits appear to occur very sparsely and rarely. All the species here in question, with the exception of *Pirola*, secrete honey. The honey-secreting organs surround the base of the ovary, or in the case of superior flowers, the base of the style. As many of the species have drooping flowers it is evidently a useful feature that several have hairs near the base of the filaments and of the petals which serve to retain the honey and to prevent intruders from entering. This is doubtless also the reason why the base of the filaments is swollen in some of the species (*Rhododendron, Ledum, Cassiope hypnoides, Andromeda polifolia, Arctostaphylos, Phyllodoce*).

All the flowers are coloured, the majority are even of a conspicuous colour. Some of them are scented (*Ledum, Pirola, Cassiope tetragona, C. hypnoides, Arctostaphylos alpina, Vaccinium uliginosum*, and (according to Bessels) *Phyllodoce*).

The pollen grains which, as is well-known, are always united into tetrads, are quite glabrous and dry; even before the buds open the pores at the apex of the anthers are generally formed, and the grains lie loosely in the air-filled pollen-sacs, even if they are not always dry enough to fall out easily. This is also the case in Denmark with *Erica Tetralix* and *Calluna vulgaris*. Exceptions to this are *Loiseleuria*, the anthers of which are of the usual kind, and *Phyllodoce*.

The sole function of the appendages, which occur on the anthers of all the species which have bell-shaped and drooping

flowers except *Lyonia, Phyllodoce,* and *Vaccinium Vitis-idæa,* must be to serve as an aid in cross-pollination; the insect will touch them and thereby shake the anthers so that the pollen falls out. The fact that in the same species either the anthers, or the appendages, or both these organs are covered with small protuberances, must have the same purpose, viz. to oppose the proboscis of the insect, and thereby increase the resulting shock. That these appendages are, on the other hand, wanting in species with open flowers which are usually more or less erect or are, at most, horizontally projecting but not drooping (*Pirola, Loiseleuria, Ledum, Rhododendron*), may easily be understood. *Vaccinium Oxycoccos* also belongs to those species in which the appendages are wanting, but its filaments are covered with hairs which perhaps serve the same end. This may apply also to *Vaccinium Vitis-idæa.*

The fact that in many species the base of the filament is very slender compared with the part just above it, appears also to be useful; it is thereby much easier for the insects to put the filament in motion and shake it, than if its base had been thick.

Arctostaphylos alpina occupies a peculiar position by reason of the fact that its appendages are short, thick and glabrous or even entirely wanting (aborted). This should be correlated with the fact that the throat is very narrow, narrower than in *A. Uva-ursi,* so that the insect must inevitably touch the filaments and shed the pollen. This is also the case in *Phyllodoce.* On comparing the above two species it will be seen that while *A. alpina* is far the better adapted for self-pollination, *A. Uva-ursi* is the better adapted for pollination by insects. In the structure of its flower *Andromeda polifolia* approaches nearest to *Arctostaphylos Uva-ursi,* especially in that the interior of its corolla is covered with erect hairs as is the case in the two species of *Arctostaphylos.* We may be justified in concluding that these hairs are connected with the

extreme narrowness of the throat: the hairs serve to gather up the pollen grains as they fall and to retain them until they either are conveyed by chance to the proboscis of an insect-visitor, or fall upon the stigma of the same flower. No species in which the corolla has a wide mouth has such hairs, because in such a case they would be superfluous. When they are wanting also in other species which have narrow throats (*Vaccinium Myrtillus, Lyonia* and *Phyllodoce* to which may be added *Erica Tetralix* and *Erica cinerea*) the reason may perhaps be found in the fact that the pores of the anthers are so near to the mouth of the flower that there would be difficulty in spreading the pollen in the interior of the corolla.

The stigma has in all the species only very small papillæ, but secretes mucilage abundantly which, in specimens preserved in spirit, appears hardened and usually filled with small vacuole-like balls. The stigma always reaches at least the level of the anthers, but usually it is higher than they and will therefore easily and immediately be able to receive the pollen which may have been brought by an insect-visitor.

On the other hand, self-pollination will in most cases be able to take place easily, as the stigma lies below the anthers, either on account of the position of the flower — in the greater number of species the mouth of the flower turns downwards — or else because the style is bent downwards, as in *Pirola*, and must inevitably in this position be dusted with the pollen when it is shed. And with regard to this point, there occurs in some Arctic species, as already shewn, a tendency to facilitate self-pollination, the distance between the pores and the stigma being shortened, and the chances of a favourable result being thereby made greater. But in regard to this, *Pirola rotundifolia* f. *grandiflora* differs from the typical form; *Vaccinium Vitis-idæa* f. *pumilum* from the typical species; and the *Phyllodoce* specimens among themselves. In *Loiseleuria* the anthers also appear to approach nearer to the stigma than they do in

the Alpine specimen. We may be justified in connecting this tendency toward self-pollination with the scarcity of insects in the country in question. It will facilitate self-pollination if the interior of the corolla by its covering of hairs is able to gather up the pollen grains and retain them as mentioned above. Some species appear to me to be less well-adapted for self-pollination, especially of *Ledum* and *Rhododendron*. The former with its richly-flowering inflorescence recalls somewhat that of the Umbelliferæ, and geitonogamy must evidently be able to take place easily in it.

All the flowers are for the most part homogamous for a long period, but some begin by being protogynous for a short time (*Arctostaphylos alpina, Cassiope hypnoides, Ledum, Phyllodoce, Loiseleuria, Rhododendron*) and others protandrous, also for a short time (*Cassiope tetragona, Vaccinium Myrtillus, V. Oxycoccos, V. uliginosum, V. Vitis-idœa*).

Probably self-pollination sometimes takes place before the flower opens, so that a kind of cleistogamy occurs, because as has been mentioned, the anthers generally open while still in the bud, and in some cases, I even found the pollen shed (*Arctostaphylos Uva-ursi*). I found the anthers dehisced, and fully developed pollen grains lying loose in the buds in this species and in the following: *Cassiope tetragona, C. hypnoides, Andromeda polifolia, Ledum palustre, Vaccinium Vitis-idœa, V. uliginosum, V. Oxycoccos, Lyonia,* as also in *Erica Tetralix, E. cinerea* and *Calluna vulgaris*. In the greater number of these species I also found that the stigma in the bud was viscid and capable of retaining the pollen, or was at least able to do so in flowers which had just expanded. In a greenhouse in Copenhagen, in a flower of *Lyonia* not yet expanded, I found pollen upon the stigma. In Finmark, in a bud of *Cassiope tetragona*, I found the stigma viscid and the anthers open; the pollen could not however fall out, but did so immediately that the anthers became dry after the expansion of the bud. This

approach to cleistogamy doubtless harmonizes well with the conditions of life under which these Arctic plants live. On the other hand it is then of but slight biological importance that the corollas are coloured and doubtless on the whole keep fresh a very long time. (On this and on Cleistogamy in *Campanula uniflora* see Warming, 1886, b, pp. 150—154.)

Of other peculiarities it is interesting to note the examples of the ovary being protected by a similar covering of hairs as are the vegetative parts, while the style is quite glabrous; here again it is two of the open-flowering species, *Ledum* and *Rhododendron*, which must be mentioned; of the others *Phyllodoce* only (and *Erica Tetralix*).

Vaccinium- and *Arctostaphylos*-species have fleshy fruits; the others have capsules. As examples of plants in which the stalk of a drooping flower rises straight into the air when the fruit becomes a capsule may be mentioned *Cassiope* and *Phyllodoce*. In the nodding capsule in *Ledum* the position of the valves is in harmony with this position of the fruit.

In all the species the flowers are undoubtedly formed the year previous to that in which they open; this has at any rate been verified in the greater number of them. They are most developed in *Arctostaphylos alpina* which is also the one to flower the earliest in spring. Considering the shortness of the summer it is evidently very useful that the development of the flowers should be spread over two years.

All the Greenland Ericaceæ have woody stems and should be referred to the growth-form called "dwarf-shrubs" (some are of decided prostrate growth, e. g. *Arctostaphylos alpina* and *A. Uva-ursi*); *Pirola* however differs most in this respect. The buds have typical scale-leaves in most of the species (*Arctostaphylos, Andromeda, Cassandra, Ledum, Vaccinium*, etc.); quite devoid of scale-leaves are *Cassiope tetragona*, the Arctic heather which extends farthest towards the north, and *Cassiope*

hypnoides. Also *Loiseleuria* has branching year's-shoots and no typical scale-leaves.

From a vegetative point of view most of these Greenland Ericineæ agree very closely with *Calluna*, their chief means of propagation being seeds; it is chiefly by the primary root that the plant absorbs food from the soil, the adventitious roots play a less prominent part in this respect. Decided deviations from this rule are the *Pirolas*, *Andromeda polifolia, Vaccinium Myrtillus, Vaccinium Vitis-idæa* and *uliginosum*, all of which have subterranean runners with elongated internodes. It is characteristic of the Ericineæ that the adventitious roots spring from the axils of leaves, above the buds.

Of all the 16 species of Ericineæ, mentioned above, two only have typical deciduous leaves, viz. *Vaccinium uliginosum* and *Vaccinium Myrtillus*. The leaves of *Arctostaphylos alpina* appear neither to fall nor to keep fresh during winter. The leaves of the other species keep fresh through at least one winter, and the ensuing spring they appear to be able to assimilate afresh; they are then found to contain starch; the leaves of some of the species can evidently keep fresh even longer.

The form of branching of the Ericineæ is rather varied. In the *Pirola*-species a racemose inflorescence generally occurs which terminates the growth of the pleiocyclic shoot; in this genus the foliage-leaves occur in a few-leaved rosette. There usually occur only subterranean lateral shoots which begin as colourless runners bearing scale-leaves (see Warming, 1884). *Pirola uniflora* is an exception (ibidem p. 86, Fig. 23). In some of the Ericaceæ the flowers occur singly in the axils of foliage-leaves (*Cassiope tetragona*), or on small dwarf-shoots which occur towards the base of the long-shoots, and bear only a few pairs of foliage-leaves, dying after setting fruit (*Calluna vulgaris*). Solitary flowers occur also in *Vaccinium Myrtillus* (for further information regarding its sympodial growth, etc., see Warming, 1884, pp. 76—77). *Vaccinium uliginosum* may

also be placed among the species which bear solitary flowers, but with some interesting variations. As in *V. Myrtillus* the apex of the shoot fails to develop, and the upper dwarf-shoots usurp its place. Each dwarf-shoot usually bears only one or two flowers which are protected by scale-leaves, but as is the case with the apices of the long-shoots, those of the dwarf-shoots also fail to develop. This species is consequently 3-axial. False dichotomy is common on account of the shoot structure.

In a great number of other Ericaceæ the vegetative shoots are likewise terminated by floral shoots, but these species are bi-axial. New shoots are developed immediately below the dying apices of the floral shoots, and are stronger the nearer they occur to the latter. The buds which occur lower down on the mother-shoot often become dormant. If many new shoots are developed it results in a dichotomy with several branches often arranged almost in a whorl, e. g. in *Ledum*; if only one or a few new lateral shoots are developed a sympodium is often formed, e. g. in *Arctostaphylos Uva-ursi*. To this division belong also *Phyllodoce, Cassiope hypnoides, Loiseleuria, Rhododendron lapponicum*, and *Vaccinium Vitis-idæa*. *Arctostaphylos alpina* belongs also to this group, although it presents certain peculiarities.

My warm thanks are due to Dr. Rendle of the British Museum for his kindness in reading the proofs of the present paper.

5—5—1908.

1.

Ericineæ (Pirolaceæ, Ericaceæ).

2. The biological anatomy of the leaves and of the stems.

By

Henning Eiler Petersen.

1908.

Introduction.

The flora of a particular country or district may in the main be divided more or less distinctly into three groups of plants, viz.: — (1) Those plants which reach their maximum in the area in question, i. e. occur as frequently as circumstances permit, or are at any rate widely distributed there; (2) those which are the advanceguards of the intruding vegetation; and lastly (3) those which are the survivors of an earlier vegetation that is now becoming extinct. Within the first group, which doubtless includes the greater part of the species occurring in the district, we may distinguish between those which have recently migrated thither, and those which are descendants of an old vegetation of the district that have adapted themselves to the climate, continually although slowly changing. Generally, when a plant migrates into a particular district we may assume that the climate of the latter suits it. But this does not imply that all the different parts of its structure are in correlation with the climate; this is not necessary, and such features may often be sought for in vain. The plant may have a protoplasm which does not require special external contrivances, as for example organs that tend to check transpiration. On the other hand it may in most cases be said of a vegetation that is dying out, that it is becoming extinct owing to the climate offering it too much opposition. In the latter case a protoplasm will be found which is less capable of resistance, as also external structures which are in every way more specialized, and which in combination with a certain lack of power in the protoplasm to adapt itself to the new conditions, are unable to maintain the life of the plant in the region in question.

Starting now from the view given above, — that a plant which migrates into a particular district need not from the first be provided with special contrivances suited to the climate of the country, but, on getting foothold in the district, will change more

or less in response to the existing climate and may adapt itself to, or be more directly influenced by, the new conditions — we must arrive at the conclusion that to ascertain the influence of the climatic factors of a particular district on its plant-world we must investigate the vegetation which is the oldest in the area, and which thrives well there at the present time. But also in this case, the lesser or greater power of the protoplasm to utilise external contrivances must be taken into consideration. If a plant needs only slight protection against, for example the danger of excessive transpiration, then of course it cannot give us any information regarding the influence of climate on the structure of plants. From the above it will be seen why it is desirable that plant-geographical studies should go hand-in-hand with studies in the lesser or greater adaptation of the plant-world to climate. Forms with a limited distribution are of course the best objects of study with regard to ascertaining the special demands of a climate over a long period, but species with a wider distribution may also be useful in regard to this point. Here it must be borne in mind that the fact of the occurrence of a species in different climates need not exclude it from being used in the above-mentioned studies. As we know, species often change their locality according to the climate, so that the different external factors in the different localities amount to the same sum total.

In regard to all plant-migrations, the power plants possess mutually to supplant each other of course plays a prominent part; therefore it may be asked, whether the components of the vegetation of any area which are becoming extinct may not in themselves reflect the existing climate of the area in question. This cannot be denied. It is however my opinion, that but rarely are plants entirely expelled from a particular area by other plants, the reason for ultimate extinction usually lying in the fact that the relationship between the life-functions or the external organs and the external factors is faulty. With regard to the influence of climate on the plant-world it must be pointed out, that it is difficult to arrive at any isolated result; the influence of a climate cannot be expressed in a single sentence, the climate not being constant itself during the year, and the plant-world not consisting of homogeneous material. Hence, the different plant-types must always be kept distinct and treated separately. To keep the influence of the individual localities distinct from the climatic factors proper is also doubtless very difficult. In beginning to enter upon studies of the kind men-

tioned frequently already, it might suffice when, as in the present paper, we are considering the anatomy of the plants, to point out how far the light-assimilatory tissues and the power of protection against the danger of excessive transpiration have been developed. In regard to these points the climatic factors will at any rate be of importance. All these studies should, however, always be followed by investigations into the influence other climates may possibly have on the plants in question.

It is with these points in view that I have taken up the present work. I am well aware that no definite result as to the influence of the climate on the Arctic plant-world can be arrived at merely by the study of the families treated here. Neither am I an authority upon Arctic climatology. I have only tried to explain the different types of adaptation and place them in their mutual relation to each other. I have attempted as far as possible to investigate the older Arctic forms, and the length of time the individual species have been in the Arctic region; but I have not succeeded in arriving at any definite conclusion regarding this point. In this connection I have been content to refer to the different geographical distributions. I shall return to this subject at the end of this paper.

The material at my disposal has not been of much service in regard to comparison with other climates. Generally, Danish specimens, wherever they occurred, have been compared with those from the Arctic regions. But there was one great drawback in regard to the Danish (North European) as well as the Arctic material — it was too scanty. It is obvious that in ample material all the variations of a plant are more likely to occur than in scanty material. By having only a few specimens for investigation there is a possibility that too great importance may be attached to variations which occur but seldom. It would have been possible for me to determine the variations which occurred in the material I had at my disposal, but owing to the fact that the habitats have not been recorded, it would have been impossible for me to enter into the reasons for the different variations; hence, I have not discussed them more fully.

I cannot say that I have brought to light any particularly new and interesting facts; the subject has been too often dealt with in regard to its main points to allow of that. The value of the present paper lies principally in the fact that a great deal of information regarding these plants has here been collected, and that the individual

species have been mutually compared. As mentioned above, the anatomy of the greater number of the plants has already been described, but I am of opinion that the present work would become too superficial if I merely referred in it to these descriptions. I have treated each species according to a certain fixed plan and this I have preferred to employ with regard also to those species which have previously been described elsewhere. In the present paper they will all be compared with each other and that by a single author who must necessarily have some definite starting point. Only in the case of *Cassiope tetragona*, upon which a small monograph has already been published, have the main points of structure been dealt with superficially.

It is chiefly the leaves and the stems which are here described, these organs being of the greatest importance in a biological, climatological connection. The roots, which occurred but sparingly in the material, have been investigated only for the sake of the mycorhiza, in the cases where this was possible. The bud-scales have not been examined at all. No attempt has been made towards giving a systematic anatomical account. The photographs of the transverse sections of the stems have been taken by Mr. A. Hesselbo. The illustrations have been drawn partly by Professor Warming and partly by me. The material consisted chiefly of specimens preserved in spirit, and was all from the Botanical Museum in Kjöbenhavn; it had been collected over a long period by different naturalists.

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Andromeda polifolia . . . . . p. 107
Arctostaphylos alpina . . . . . p. 115
— *Uva-ursi* . . . . . p. 112
(*Bryanthus coeruleus*) . . . . . p. 99
(*Cassandra calyculata*) . . . . . p. 110

Cassiope hypnoides . . . . . p. 105
— *tetragona* . . . . . p. 101
Chimophila umbellata . . . . . p. 87
Ledum palustre . . . . . p. 91
Loiseleuria procumbens . . . . . p. 96
Lyonia calyculata . . . . . p. 110
(*Oxycoccos palustris*) . . . . . p. 118
Phyllodoce coerulea . . . . . p. 99
Pirola grandiflora . . . . . p. 80
— *minor* . . . . . p. 83
— *rotundifolia* . . . . . p. 80
— *uniflora* . . . . . p. 86
— *secunda* . . . . . p. 84
Rhododendron lapponicum . . . . . p. 89
Vaccinium Myrtillus . . . . . p. 127
Vaccinium Oxycoccos . . . . . p. 118
— *uliginosum* . . . . . p. 123
— *Vitis-idæa* . . . . . p. 121

Anatomical description of the different species.

Pirolaceæ.

Pirola grandiflora Rad.

Syn. *Pirola rotundifolia* v. *grandiflora* DC.

Warming, 1885, p. 16. Stenström, 1895, p. 137 (cf. fig.)

Material examined from: — West Greenland: tent 16 (Ryder); Sarfanguak; Godhavn; Upernivik; Kangerdluarsuk. East Greenland: Cape Stewart.

The leaf (Fig. 1). The outer walls of the epidermis are fairly thick, cuticularized beneath the cuticle, and thickened especially on the upper surface of the leaf. Lateral walls undulating, irregularly thickened, furnished with numerous pores. Hairs are absent. Stomata are confined to the lower surface; they project slightly. The epidermis of the lower surface contains chlorophyll grains. Distinct palisade-tissue does not occur; in form, the upper cells of the mesophyll correspond

more closely to the other cells, with perhaps less tendency to a lobate form, but like them they consist of more or less irregular, rounded, parenchymatous cells. The lobes mentioned above characterize more particularly the central and lower cells of the mesophyll, and are seen most distinctly in the transverse and longitudinal section; in surface section the cells of the mesophyll are irregular, but no lobes can be seen. In surface section the intercellular spaces, which never attain any considerable size, are sharply defined and shew transparent in contrast with the brownish colour (in spirit-material) of the cells of the mesophyll; they are smaller

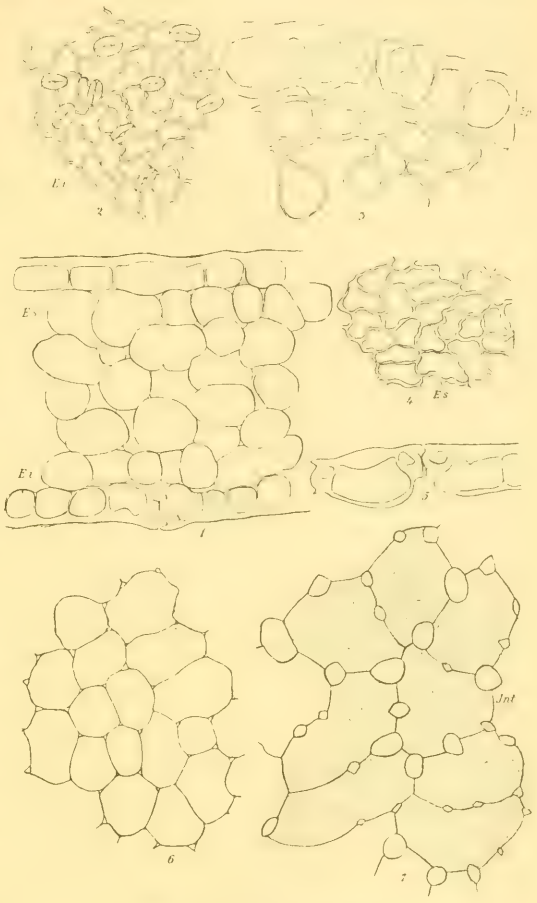

Fig. 1. *Pirola grandiflora.*

1, Leaf in transverse section. *2*, The epidermis of the lower surface. *3*, Hydathode. *4*, The epidermis of the upper surface. *5*, Stoma. *6*, Horizontal section through the mesophyll which answers to the palisade-layer. *7*, Horizontal section through the lower cells of the mesophyll. The peculiar intercellular spaces should be noted. (Hab. several places in Greenland; *1* is from Upernivik). (H. E. P.)

The letters which accompany the figures indicate the same everywhere: — *Ep*, epidermis; *Ei*, the epidermis of the lower surface; *Es*, the epidermis of the upper surface; *Chl*, chlorophyll grain; *pa*, palisade-tissue; *Jnt*, intercellular space. The upper and lower epidermis seen from the surface are drawn always with the same magnification in regard to each species.

and fewer in number towards the upper surface of the leaf, larger and more numerous towards the lower surface of the leaf, where the mesophyll may begin to resemble spongy parenchyma, but cannot actually be termed spongy parenchyma. Especially in this part of the leaf the intercellular spaces impress one as rather curious, as it appears that they are not formed normally between 2—3 or more cell-walls, but by the walls of two adjoining cells separating from each other (Fig. 1, 7). That this can really be the case may be proved by comparing the corresponding circumstances in *Pir. secunda* (Fig. 3, 2). Here we are undoubtedly dealing with a kind of secondary intercellular-space-formation. All the cells of the leaf give the reaction for tannin, but least is given by the central cells of the mesophyll. In this point the Greenland specimens of this species differ from the Danish individuals of *Pir. rotundifolia* which is otherwise very closely related to *Pir. grandiflora*; the Danish *Pir. rotundifolia* has cells in the centre of the mesophyll which are entirely devoid of tannin, forming a distinctly transparent, central area. There is no stereom developed around the veins of the leaves. Hydathodes occur over the termination of the vascular bundles (Fig. 1, 3).

The stem. From a biological point of view the structure of the stem presents no feature of any great interest. In the young stem a layer of cortical cells occurs under the epidermis — thick-walled like the latter, and devoid of starch. When the primary epidermis falls off, a kind of cork is formed consisting of angular cortical cells. There is no regular periphery, but the older formations persist for a long time. The other parts of the structure of the stem present no point of interest beyond the fact that the inner cortex consists of large parenchymatous cells, abundantly filled with starch, and that annual rings may occur in the central cylinder.

The root has endotrophic hyphæ in its outer cells.

There is probably no other difference between the Danish *Pir. rotundifolia* and the Greenland *grandiflora* form than the one mentioned above.

Pirola minor L. (Fig. 2.)

Warming, 1897, p. 103. Stenström, 1895, p. 137 (cf. fig.).

Finmark: Alten. Färöes: Bordö.

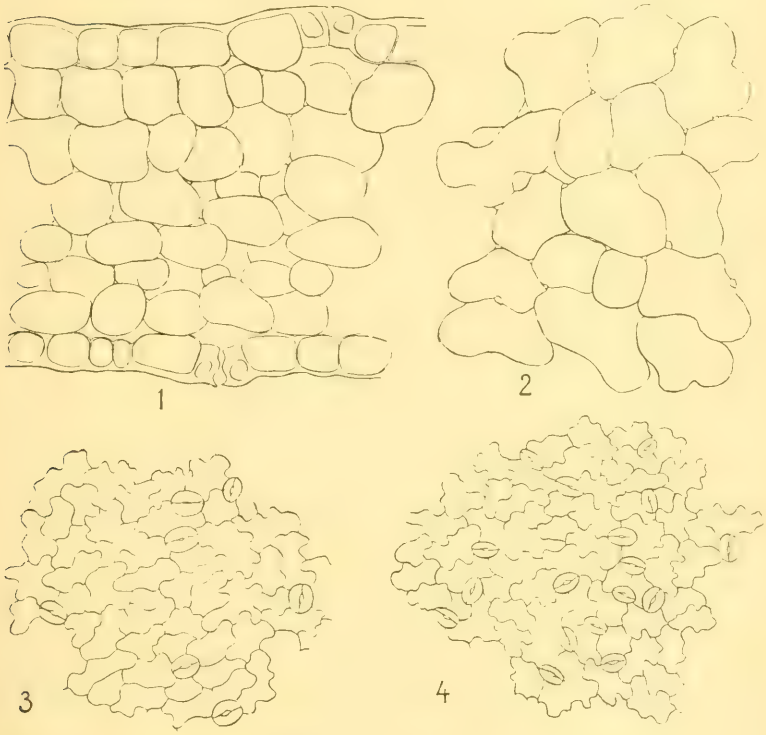

Fig. 2. *Pirola minor.*

1, Leaf in transverse section. *2*, The mesophyll near the epidermis of the upper surface. *3*, The epidermis of the upper, *4*, of the lower surface (Finmark). (H. E. P.)

The leaf resembles in its main points that of *Pir. grandiflora*. As differences of importance may be mentioned that stomata occur on the upper surface of the leaf, but are fewer in number than those of the lower surface, and are slightly

projecting; also in the present case cells distinctly devoid of tannin occur in the middle of the mesophyll. The epidermis of the lower surface contains chlorophyll grains as in *grandiflora*. Warming has described in his paper, Exkursionen til Skagen i Juli 1896 (see above), the anatomy of the leaf of this species. He mentions a rather peculiar fact in regard to the stomata. On the leaves of "light-plants" (from the Danish downs) these organs cease to be functional at an early date, so that they occur on older leaves as useless structures, but in "shade-plants" (from woods: Tidsvilde Hegn, and Hornbæk Plantage) they are well-developed and function normally. The specimens which I have examined and which are from Finland and the Färöes come nearest to the Danish wood-forms in this respect. The stomata do not occur especially along the veins as in *Pir. grandiflora*. In all other points it resembles *Pir. grandiflora*.

I have made no examination of the roots.

Pirola secunda L. (Fig. 3).

Of this species I have had for examination only spirit-material from Disco (Porsild) and from Denmark. Further I have investigated herbarium-specimens from Holstensborg in Greenland, and Asbirgi in Iceland.

The structure of the leaf corresponds in the main points with that of *Pir. grandiflora* and of *minor*.

The upper and lower epidermis are somewhat thicker than in these forms. Stomata occur on both sides, but are fewer in number on the upper surface, as is the case in *Pir. minor*. On the latter surface the stomata are especially confined to the area near the veins of the leaves. Both the upper and lower epidermis contain chlorophyll grains. Hydathodes occur, but hairs are absent.

The cells of the mesophyll are of the same form as those of the mesophyll in the two above-mentioned species. No cells

devoid of chlorophyll occur. The intercellular spaces are in many cases formed by the separation of two neighbouring membranes and not normally either between three cells or between the lobes of two as may be conjectured to be the case in *Pir. grandiflora* and in *minor*. In regard to the

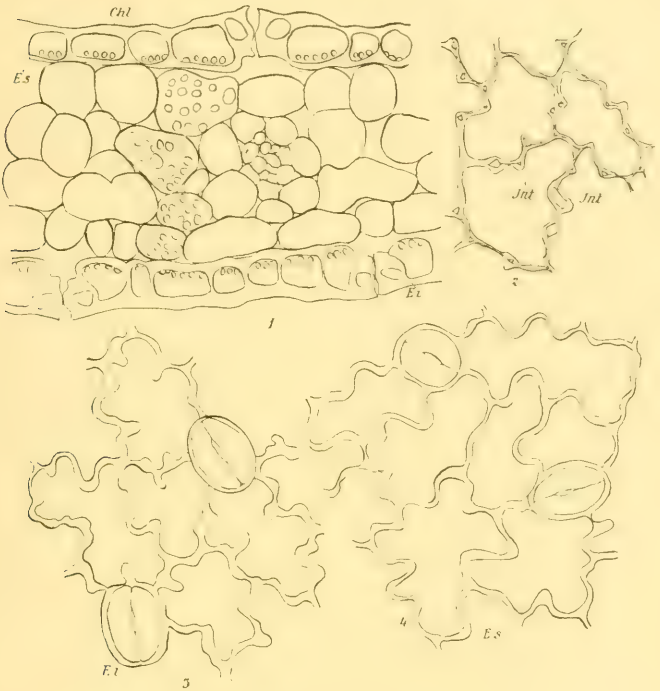

Fig. 3. *Pirola secunda.*

1, Leaf in transverse section. *2*, Lower mesophyll with the characteristic intercellular spaces. *3*, The epidermis of the lower, *4*, of the upper surface. × about 430. (Denmark: Hornbæk Plantage). (H. E. P.)

structure of the leaves the two northern specimens agree exactly with those from Denmark.

The structure of the stem presents no feature of importance it corresponds essentially with that of the two mentioned above.

No examination has been made of the roots.

Pirola uniflora L. (Fig. 4.)

The specimens are from Finmark: Alten (July 6, 1885, Warming). The Danish specimens are from Tidsvilde Hegn and from Hornbæk Plantage.

This species differs from the three described above in regard to the leaf, the inner structure of the latter being much more dorsiventral, and arranged on the whole in a typical manner.

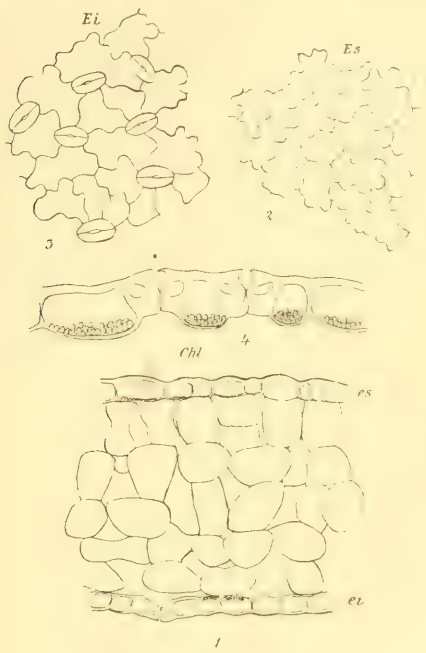

Fig. 4. *Pirola uniflora.*

1, Leaf in transverse section; below the epidermis of the upper surface (*es*) a palisade-like layer of cells is seen. Cf. note p. 81. *1*, *2* and *3*, × about 120; *4* × about 250. (Finmark: Alten) (H. E. P.)

The epidermis of the upper and lower surface have only slightly thickened outer walls and much undulating lateral walls. Stomata occur only on the lower surface and are slightly projecting. Hairs are absent. Chlorophyll grains occur in both the upper and lower epidermis.

The upper layer of the mesophyll is of palisade-form, and the cells are short and broad; the rest of the mesophyll is loosely arranged with large intercellular spaces, and consists as usual of irregularly rounded thin-walled cells which branch but slightly and are colourless in the spirit-material. In Danish specimens the palisade-cells were somewhat longer and more slender than in the specimens from Alten, otherwise there was no especial difference between them.

The stem and the roots have not been particularly examined.

[**Chimophila umbellata** (L.) DC. (Fig. 5.)

Material is at my disposal only from the wood "Sandflugts-plantage" at Rönne in Bornholm.

This species, the leaves of which are coriaceous, presents quite a different type of leaf from those of the three mentioned above. It stands in the same relation to *Pirola uniflora* as *Arctostaphylos Uva-ursi* does to *Vaccinium Myrtillus*.

The leaf is dorsiventral with thick outer layers in the epidermis, consisting of a thickened cuticle and cuticularized layer. Stomata occur only on the lower surface and on a level with the epidermis. Hairs are absent; starch occurs in both the upper and the lower epidermis.

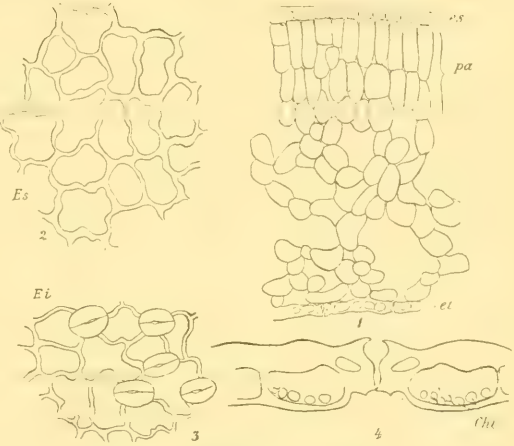

Fig. 5. *Chimophila umbellata.*
Cf. note p. 81. (Bornholm: Rönne.) (H. E. P.)

The palisade-tissue consists of from two to three layers of cells. The structure of the spongy parenchyma is loose and it consists of elongated cells, elongated more or less in the direction of the length of the leaf. Hydathodes are absent.

Annual rings are distinctly visible in the stem. Petersen, p. 72; Segerstedt, pp. 35—37.

The roots have not been investigated.]

Of the above five species only *Pirola grandiflora* and

Pirola minor occur in the Arctic regions. If the three other species be mentioned in order of their relation to the Arctic region, *Pirola uniflora* and *secunda* come first and *Chimophila umbellata* comes last. On grouping these five species according to the xerophilous structure of their leaves — they are all evergreens — then *Chimophila* is the most xerophilous and *Pirola uniflora* the least. There need not necessarily be anything peculiar in this. The reason why the purely Arctic form *Pir. grandiflora*, as also *Pirola minor* and *secunda* (as regards *Pir. uniflora* see below), do not present any especially xerophilous characters is that these three forms being saprophytes are subject to quite different conditions from those of the autophytes and consequently they cannot in so high a degree as the latter offer resistance to external factors such as wind and weather. The view that these latter plants are more independent has been put forward by Warming (Biol. opt. p. 36) according to whom it was first given by Heinricher.

The structure of *Pirola uniflora* is not xerophilous, but it is reported to have evergreen leaves. There must be some cause underlying this, as the structure of the leaves is exactly that of a deciduous leaf. Possibly some saprophytic circumstance is connected with this. The species is not entirely Arctic and lives in Finmark under conditions which do not occur in Arctic regions (viz. as a woodland-plant). In spite of its xerophilous structure *Chimophila* is not an Arctic plant. Thus the *Pirolaceæ* cannot be said to make any special contribution towards the interpretation of the influence of Arctic climate upon plant-structure.[1]

[1] A general account of the Ericaceæ is given in a separate section at the end of this paper.

Ericaceæ.

Rhododendron lapponicum Wahlenb. (Figs. 6—8.)

Warming, 1887, pp. 111—12; 1885, pp. 35—36. Börgesen, 1890, pp. 236—37. Ambronn, 1980, p. 71. O. G. Petersen, 1901, p. 78.

I have had specimens for investigation from the following localities: — West Greenland: Kakortok (June 6, 1887); Adglumersat (June 11, Kornerup); Tatsip-ata (July 15, 1884, Th. Holm); Umanaptimilia (Juli 17, 1887, C. Ryder). East Greenland: Hekla Havn (November 4, 1891, N. Hartz); Finmark: Alten (1885, E. W.).

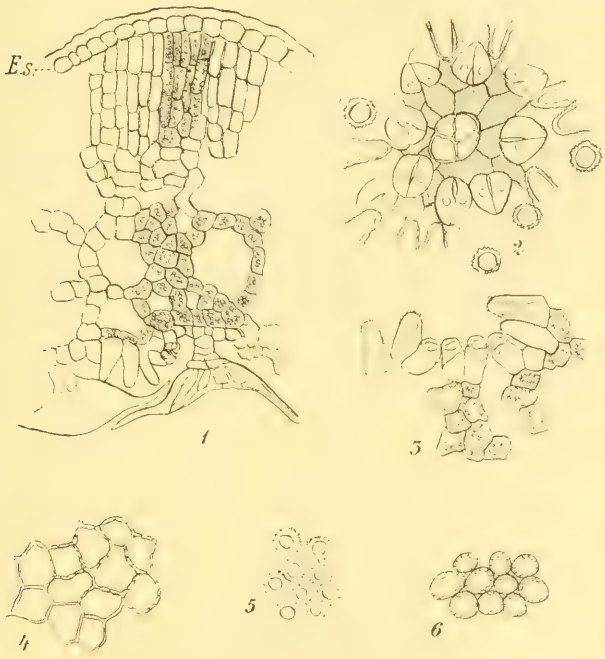

Fig. 6. *Rhododendron lapponicum.*

1, Leaf in transverse section. *2*, Epidermis with stomata below a peltate hair. *3*, Stoma in transverse section. *4*, The epidermis of the upper surface. *5*, The papillæ of the lower epidermis in surface view. *6*, Palisade-cells seen from above. (E. Warming.)

The leaf. The epidermis of the upper surface is much thickened by the presence of a thick cuticle and beneath it a cuticu-

larized layer, and is sparingly covered with large peltate hairs. The lateral walls are almost polygonal. An inner membrane is often seen to have separated from the inner walls of the cells of the epidermis giving an impression that we are here dealing with an inner mucilaginous wall (Fig. 7). But such a structure I have not been able to demonstrate with any certainty. In a few cases I further observed that a similar structure was found in connection with the upper margin of the cells. It is possible that the spaces thereby formed contain a fluid which serves as a protection against the danger of excessive transpiration. In some cases I observed starch — or properly speaking chlorophyll grains with starch — in the upper epidermal cells. The lower epidermis is strongly papillose, each cell-cavity terminating in a papilla. These papillæ have at their apex a cuticle which is slightly rough with prickles. The stomata are confined to the lower surface of the leaf, and, as is well-known from Warming's description (l. c. p. 112 and Fig. 8 in Om Gronlands Vegetation), they all occur beneath the peltate hairs with which the whole of the lower surface is thickly covered. Upon the inner side of the guard-cells and upon the nearest adjacent cells a cuticularized outer layer may be seen.

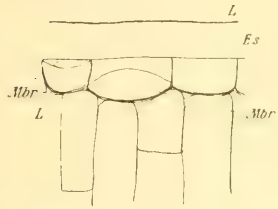

Fig. 7. *Rhododendron lapponicum.*

Mbr, Membranes. *L*, Lumen. This figure shews indications of the mucilaginous walls which occur in this species (Greenland). (H. E. P.)

The palisade-cells occur in 5 to 6 layers, and are small (at most about 50 μ) and diminish in height towards the interior; they constitute about one-third the thickness of the leaf. The spongy parenchyma consists of non-branching cells, united into lamellæ that stand at right angles to the longitudinal axis of the leaf. Very large intercellular spaces occur between the lamellæ. Below the vascular bundles may be seen indications of aqueous-tissue.

The leaf is strongly protected especially by its peltate hairs.

The stem. The primary cortex consists of homogeneous, rounded cells, with larger or smaller intercellular spaces, and a thick epidermis. The secondary cortex consists of ordinary cork-cells.

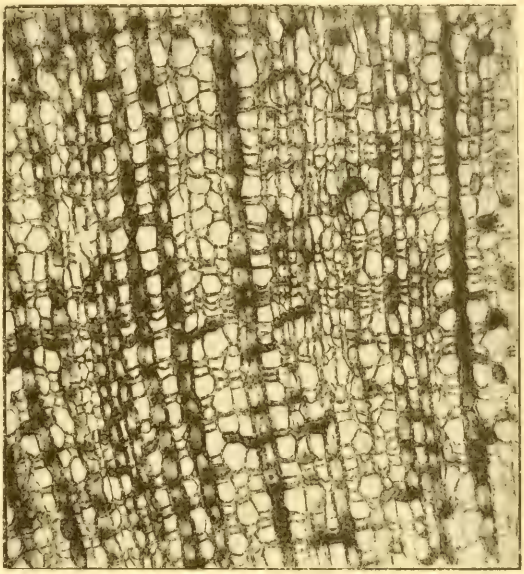

Fig. 8. *Rhododendron lapponicum.*
Stem in transverse section (Greenland). × 180. (Phot.)

There is no great difference between the spring and summer wood, and the limits between the different annual rings are not very distinct. Besides the actual limits of the annular rings, which may be verified by calculating the age of the portion of the branch in question from the number of its shoots, some confused boundary lines may often be discerned within the cortical zone of growth (O. G. Petersen, p. 78; Ambronn, 1890, p. 71).

I have not examined the roots.

Ledum palustre L.

with f. *decumbens* Ait. and f. *groenlandica* (Oed.). (Figs. 9—12.)

This species, whose occurrence in the Arctic regions is as frequent as is that of *Rhododendron lapponicum*, is, like the latter, specially characterized by the fact of its leaves being excellently protected.

Warming, 1887, p. 109; idem., 1885, pp. 39—42. Börgesen, 1895, pp. 236—237. Lidforss, 1907, p. 75. Segerstedt, 1894, p. 22. Ambronn, 1890, p. 71. O. G. Petersen, 1901, p. 78. Abromeit, 1899, p. 54.

I have had specimens for investigation from the following localities: — West Greenland: Sukkertoppen (Aug. 16, 1884, E.W.); Amarortalik (July 30, 1884, E. W.); loc. ign. (July 11, 1884 and July 28, 1885, S. Hansen). Finmark: Bosekop (E. W.).

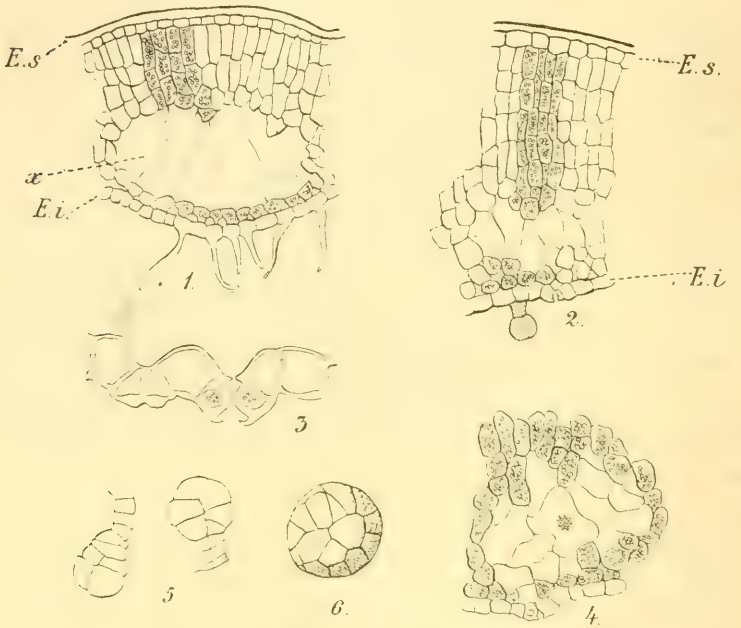

Fig. 9. *Ledum palustre* var. *decumbens*.

1, 2, Transverse sections through different parts of the leaf. *x*, Transparent cells. *3*, Stoma. *4*, Spongy parenchyma shewing the transparent cells. *5, 6*, Glandular hairs seen laterally and from above. (E. Warming.)

The leaf. The epidermis of the upper surface has much thickened outer walls with cuticle, and beneath that a cuticularized layer; the lateral walls are polygonal and have pores; a few glandular hairs occur. The outer walls of the lower epidermis are less thickened on account of the dense hairiness of this surface. According to Lidforss, chlorophyll grains occur in the upper

epidermis. There are four kinds of hairs: — 1, unicellular hairs (one kind) with a thick suberised membrane which is of importance only on older leaves, 2, multicellular hairs, *a*, long and filiform, and consisting of two rows of long, narrow cells, *b*, two kinds of glandular hairs with larger or smaller multicellular apices upon a many-celled stalk. Only the larger glandular hairs occur on the upper surface (I cannot help thinking that Börgesen (1890) in his Fig. 1 has confused the two kinds of glandular hairs. Fig. 1, *f*, shews the last stage of the one kind of glandular hair; *i*, the last stage of the other; and *g*, shews a medium stage in the development of the large hairs which have not been investigated in their younger stages). The stomata, which are not protected by any special kind of hairs but by the continuous covering of hairs, are confined to the lower surface and project slightly. They are so orientated that the transverse section of the leaf does not give the usual view of the stomata, which may be had either in longitudinal or oblique section. This orientation of these organs occurs especially in forms with furrows; but, as is well-known, *Ledum* approaches these forms by the fact of its being able to roll in its leaves to some extent. The inner sides of the guard-cells, as also the neighbouring cells of the mesophyll, have a cuticularized outer membrane. In regard to *L. groenlandicum*, the palisade-tissue consists

Fig. 10. *Ledum palustre.*

1, Leaf in transverse section. *x*, Transparent cells in the process of disorganization. *Sv.* Spongy parenchyma. *2*, The tissue below the central vascular bundle of the leaf. *y*. Transparent cells in the process of disorganization. *7*, Thick-walled cells like those in *Andromeda* (Greenland: Sukkertoppen). (H. E. P.)

usually of only 2—3 layers, but in *L. palustre* frequently of from 5 to 6 layers of palisade-cells of medium height.

The spongy parenchyma, which comprises about one-half of the thickness of the leaf, consists in the older leaves of cells which are either non-branching or branch only slightly, and which unite so as to form intercellular spaces at fairly

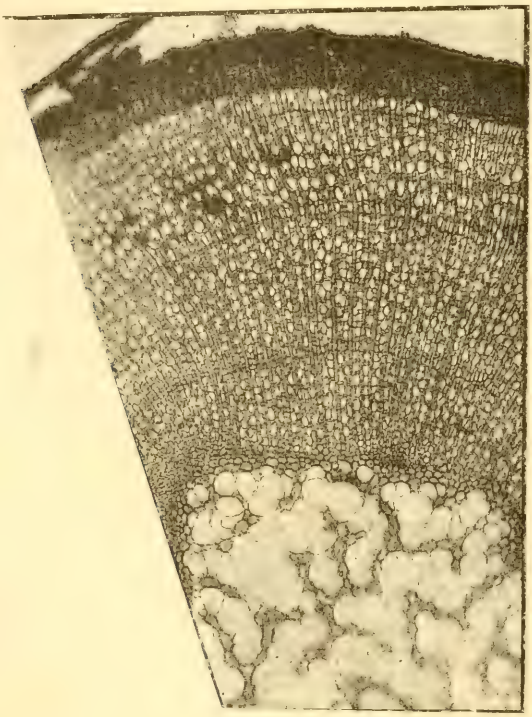

Fig. 11. *Ledum palustre.*
Stem in transverse section; slightly mag. (Greenland). (Phot.)

regular intervals. In these spaces, in older leaves, traces of a previous tissue may be found in the form of empty cells or portions of cell-walls. In the young leaves these spaces are entirely filled with a closely-packed tissue consisting of transparent cells which are doubtless filled with cell-sap and which perhaps serve as reservoirs of water and are of importance as

a protection against excessive transpiration (Fig. 10, 1; Fig. 9, 1, 2, 4). By the disorganization of these cells the large intercellular spaces are formed. Below the vascular bundle, which contains but very little stereom, a tissue occurs consisting of transparent cells (Fig. 10, 2) which have far greater power of offering resistance to external factors than those in the spongy parenchyma and which resemble those that occur in *Andromeda*, but are not so compact and have not the interspersed thick-walled cells, occurring either singly or in trabeculæ. The leaf varies greatly in thickness and breadth, sometimes it is thick and narrow (*palustre*), sometimes thin and broad (*groenlandicum*), but besides this there exist hardly any differences of importance.

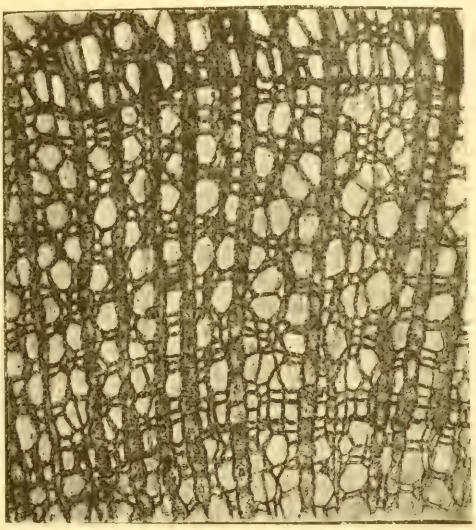

Fig. 12. *Ledum palustre.*
Stem in transverse section; the limits of two annual rings are discernable; × 180. (Greenland). (Phot.)

The stem. The primary cortex consists of a zone of small cells which occur just within the epidermis, which is hairy like the leaf and fairly thick-walled; internal to these are transparent, thin-walled cells mixed with a few with thicker walls, and trabeculæ of such thick-walled cells; while most internal are one to several rows of cells of the same form as the outermost ones. The pith, consists partly of transparent, thin-walled cells and partly of thick-walled cells, the latter occurring as trabeculæ between the former.

The secondary cortex, which according to Segerstedt is

developed on the lower parts of the year's shoots, is formed of cork-tissue in the customary manner (Segerstedt p. 29).

There is no difference between the elements of the spring and summer wood (O. G. Petersen, p. 78); the limits of the different annual rings are sharply defined, but it is difficult to decide where each annual ring begins (Fig. 16). If the thick line seen in Fig. 9 indicates the completion of the annual ring then the wood first formed is unusually marked and small-celled, if not then it is difficult to explain the presence of this line.

I have not examined the roots. (Hesselman, p. 27).

Loiseleuria procumbens (L.) Desv. (Figs. 13—14).

Warming, 1885, p. 31; idem., 1887, p. 111. Börgesen, 1895, pp. 236—237. Ambronn, 1890, p. 70. Tedin, 1892, p. 75. O. G. Petersen, 1901, p. 78.

I have had specimens for investigation from the following localities: — West Greenland: Godthaab (June 28, 1884, Th. Holm); loc. ign. (July 28—30, 1885); tent 17 (Aug. 30, 1886, Ryder); tent 14 (July 13, 1887, Ryder); Finmark: Tromsö (June 28, 1885, E. W.); Bosekop (July 3, 1885, E. W.). Iceland: Mossfellsheidi (June 14, 1895). Norway: Tronfiæld (F. Börgesen); Storlien (F. Börgesen).

The leaf is subericoidal. The margins of the leaves are somewhat bent inwards, and as the midrib stands out conspicuously on the lower surface a kind of furrow is formed on either side of the midrib.

The upper and lower epidermis are very much thickened by the presence of a cuticle and beneath it a cuticularized layer except in such places between the margin of the leaf and the central ridge where protective, unicellular hairs occur. The epidermis is however thicker in this plant than in *Bryanthus*. Mucilaginous membranes are seen in the inner wall of the cells of the epidermis, on their surface and sides (but not in

those of the central ridge) (cf. Fig. 6, p. 5, in Warming's Om Grönlands Vegetation). According to Lidforss, chlorophyll grains occur in the upper epidermis. The stomata occur only beneath the hairs on the lower surface, and are arranged obliquely and project slightly. The palisade-cells occur in 3—4 layers and are slightly oblique; length (at most) about 60 μ.

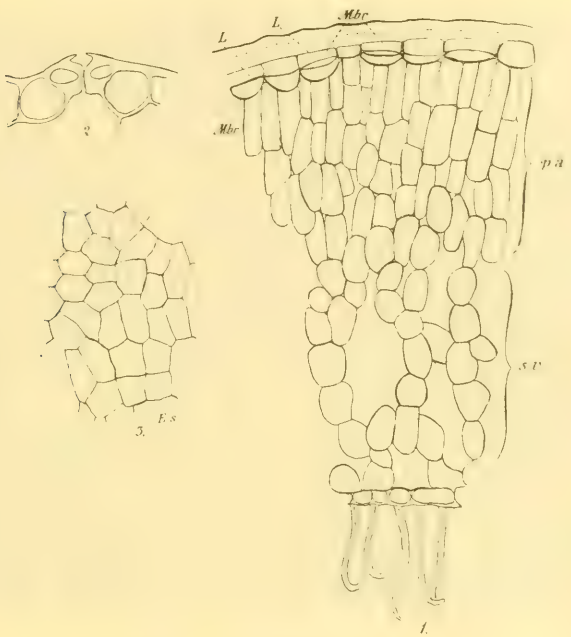

Fig. 13. *Loiseleuria procumbens.*

The leaf. *1*, Transverse section. *2*, Stoma. *3*, The epidermis of the outer surface. *Mbr*, Membrane. *L*, Lumen. (*1*, Greenland: Tugtokortok.) (H. E. P.)

The spongy tissue consists of ordinary, slightly-branching parenchymatous cells, fairly thick-walled, and most developed in a vertical direction; it has large intercellular spaces, which also occur below the vascular bundle in the central ridge on the lower surface. Stereom slightly developed.

The stem. The primary cortex (Tedin, 1892, p. 75) within the epidermal layer varies in thickness and consists of large,

transparent cells interrupted by trabeculæ of thicker-walled cells with contents; these are not, however, as distinctly developed as in *Andromeda* and *Ledum*. The primary cortex falls off very early, even by the end of the first year. The outermost part of the secondary cortex consists of an ordinary cork-tissue of no importance.

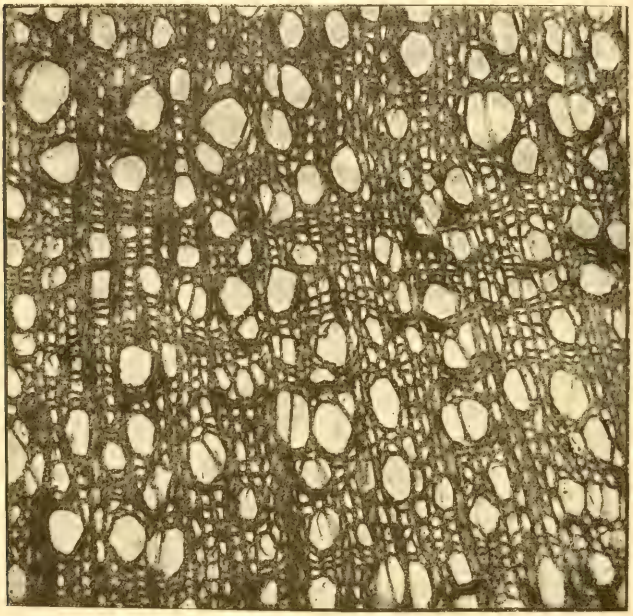

Fig. 14. *Loiseleuria procumbens.*
Transverse section of stem; several annual rings are discernable. × 180. (Greenland.) (Phot.)

The annual growth of the wood is rather difficult to demonstrate, because, as it appears, lines are formed in the annual wood which resemble annual rings, but they can scarcely be such. In some cases the annual rings are however distinct. The spring wood is fairly sharply differentiated from that of the summer (or autumn) (O. G. Petersen, p. 78).

I had no material of the root for investigation.

Phyllodoce coerulea (L.) Gren. & Godr. (Figs. 15—17.)

Phyllodoce taxifolia Salisb. *Bryanthus coeruleus* (L.) Dippel.

Warming, 1885, p. 20; idem, 1887, p. 109. Börgesen, 1895, pp. 234—35. Ambronn, 1890, p. 71. O. G. Petersen, 1901, p. 80. Kihlman, 1890, p. 232.

I have had specimens for investigation from the following localities: — West Greenland: Sukkertoppen (July 5, 1884, Th. Holm); Tatsip-ata (July 15, 1884, Th. Holm); loc. ign. (July 20, 1884, S. Hansen). East Greenland: loc. ign. (Aug. 1892), Dronning Louises Ø. Norway: (Finmark) Bosekop (1885, E. W.); (Dovre) Vaarstien (July 13, E. W.); Storlien (July 20, 1894, F. Börgesen); Lille Elvedal (July 11, 1887). [Sweden: Härjedalen].

The leaf is rounded, triangular in transverse section, and furnished with two furrows, one on either side of a central ridge, in which furrows the stomata occur. The epidermis outside the furrows is very much thickened and has no mucilaginous inner walls like those in *Loiseleuria* and the lateral walls are roundly angular; in a few cases chlorophyll grains occur in this part of the epidermis (Lidforss, p. 75). In the furrows the epidermis is thin and has very prominent stomata which are rather thickly covered with two kinds of hairs — unicellular bristles, and multicellular, glandular hairs. The stomata are placed obliquely to the longitudinal axis of the leaf, as in the case of ericoid leaves with furrows.

Fig. 15. *Phyllodoce coerulea.*
The leaf. *1*, Epidermis of the outer surface. *2*, Stoma. (*1*, East Greenland; *2*, West Greenland.) (H. E. P.)

The palisade-tissue consists of from 1 to 2 layers of cells as much as 70 μ in height; they are longest in the specimens from Härjedalen. The spongy parenchyma is relatively large — comparatively larger in this species than in *Loiseleuria* — and consists of non-branching or slightly branching cells elongated in various directions and not, as is usual in *Loiseleuria*, elongated chiefly transversely. Large intercellular spaces occur, owing to the form of the leaf and to the fact that the stomata

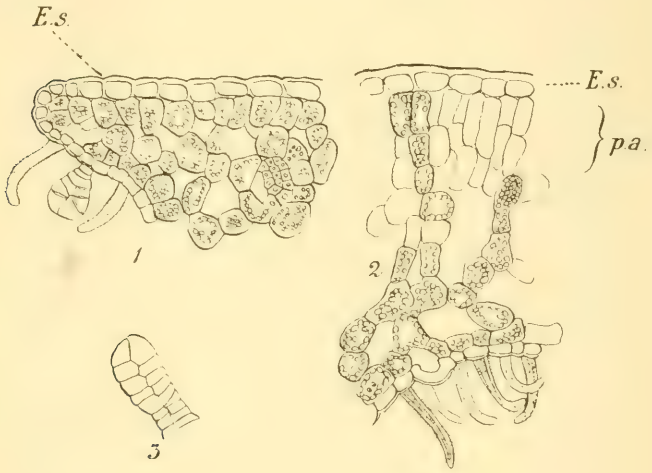

Fig. 16. *Phyllodoce coerulea.*
The leaf. *1*, *2*, Transverse section. *3*, Multicellular hair.
(Greenland: Sukkertoppen.) (E. Warming.)

are well protected. No especial stereom nor aqueous tissue occur.

The stem. The primary cortex has a thick epidermis with the same kind of hairs as on the leaf, and consists of transparent cells with thick walls which occur either singly or in trabeculæ. The pith has a similar structure. The primary cortex persists during the first and partly during the second year. The secondary cortex is formed by both regular and irregular cork-tissues which exhibit no point of interest. The

annual rings are on the whole fairly distinct and the spring wood is differentiated from that of the summer.

The roots have not been investigated.

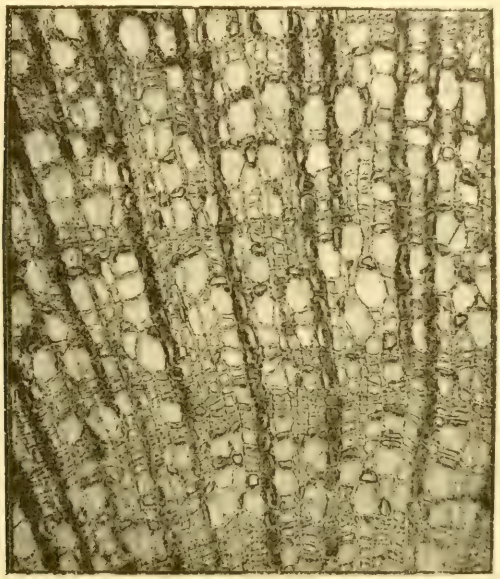

Fig. 17. *Phyllodoce coerulea.*
Transverse section of stem. × 180. (Greenland.) (Phot.)

Cassiope tetragona (L.) Don. (Figs. 18—21.)

Warming, 1885, pp. 53—54; 1887, p. 108. Linsbauer, 1900. Börgesen, 1895, pp. 236—237. Ambronn, 1890, p. 70. O. G. Petersen, 1901, p. 76.

The specimens I have had for examination are from the following localities: — West Greenland: Tatsip-ata (July 15, 1884, Th. Holm); (Disco) Röde Elv (Porsild); Kekertat (Sept. 9, 1886); Pugtokortok (July 13, 1887, C. Ryder); Pröven (July 2, 1888, C. Myhre); Upernivik (July 11, 1886); tent 20 (Ryder); loc. ign. (July 14, 1884). East Greenland: Danmarks Ö (Nov. 6. 1881,

N. Hartz); loc. ign. (July 6, 1892, N. Hartz). Spitzbergen: Tempelbay (July 17, 1882, Nathorst). Norway: Palvand (F. Börgesen).

The anatomy of this form has recently been exhaustively investigated by K. Linsbauer; therefore I shall here make only a few supplementary remarks. Stomata may occur on the upper

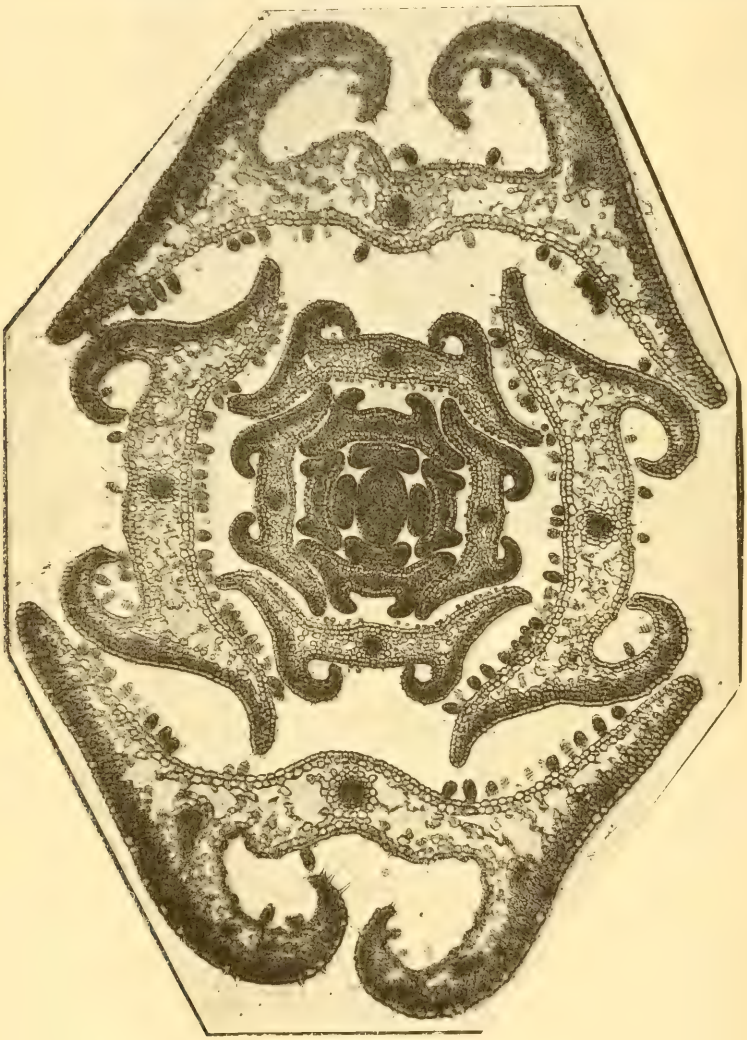

Fig. 18. *Cassiope tetragona.*
Microtome-section through a bud. (Phot.)

surface of the leaf, that side of the leaf which is pressed close to the stem. Upon the two sides of the leaf, the parts of the palisade, which form the limit of the air-cavities, are often very unequally developed (Fig. 20), so that the layers of palisade-cells differ rather considerably in number. This difference is most obvious in such parts of the leaf as have not been covered by other leaves, consequently, especially towards the apex of the leaf (Fig. 20, 1 and 2). This may be explained by the fact that the palisade-cells are formed in the bud, the leaves of which overlap each other considerably, leaving the

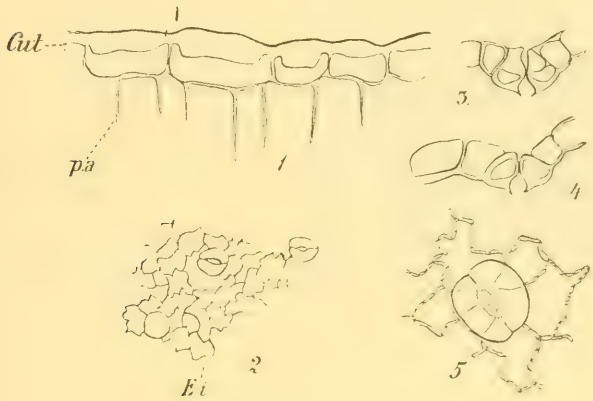

Fig. 19. *Cassiope tetragona.*
The leaf. *1*, The outer epidermis with cuticle. *2*, Inner epidermis with stomata. *3—5*, Stomata. (E. Warming.)

apices free. It may be proved that the part of the four longitudinal layers of the palisade-tissue which is most well-developed, corresponds with the direction in which the light falls most intensely. Symmetrically-developed flanks occur not only in places where the leaves have overlapped each other, but also on such leaves as have been placed symmetrically towards the light.

I observed the Kraus winter-condition in a specimen from Danmarks Ö (Greenland; N. Hartz). Like Linsbauer I have not

been able to find any annual rings in the material at my disposal.

On the whole the leaf of *Cassiope tetragona* is of very peculiar structure. By the erect position of the leaves and by their close adhesion to the stem, their surface has no doubt been greatly reduced, a fact which must be extremely favourable in cases of continuous drought. The consequent danger to the stomata, viz. that they are now turned directly towards the

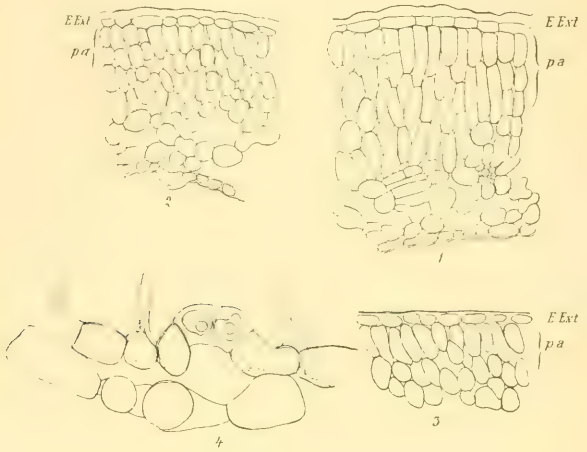

Fig. 20. *Cassiope tetragona.*

The leaf. *1* and *2* shew the difference which may occur in the development of the two flanks when the light does not act with the same degree of intensity upon both of them. *3*, Slanting palisade-cells. *4*. Stoma. (Greenland.) (H. E. P.)

wind, is very happily avoided by the growth of the margins of the leaves. The stomata are situated in the interior of a relatively large air-cavity, a fact which greatly checks all movement of air. The thin epidermis which lines this cavity, as also the large intercellular spaces of the leaf resulting from the form of the leaf and the position of the palisade-cells, bear witness to the great protection afforded by this air-cavity. It is evident that it must be of vital importance to a leaf that persists through the winter that it should prevent too much dry air from entering into its interior, which would certainly happen in a

very high degree, if it had intercellular spaces which were not protected. In regard to leaves which persist for several years, it may be said that the degree of protection is without doubt in proportion to the size of the air-cavity. To what degree the air-cavity and the large intercellular spaces serve to utilize the oxygen formed by assimilation of the carbonic acid formed by respiration I am not able to say. The leaf is also protected by different kinds of hairs (cf., e. g., Warming, Biol. Optegnelser, p. 53).

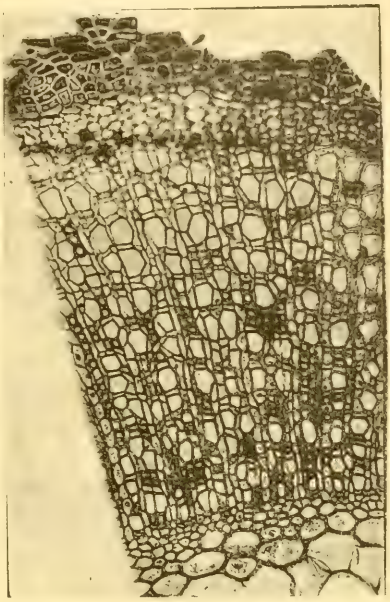

Fig. 21. *Cassiope tetragona.* Stem. × 180. (Phot.)

Jungner's[1] theories regarding the importance of the form of the leaf may doubtless be regarded as extremely fanciful.

Cassiope hypnoides (L.) Don. (Fig. 22.)

Börgesen, 1895, pp. 236—237. Tedin, 1892, p. 75. Hesselman, 1900, p. 27.

The specimens I have had for investigation are from the following localities: — West Greenland: tent 16 (July 28, 1887, C. Ryder); loc. ign. (Aug. 1, 1892). East Greenland: Dronning Louises Ø (Aug. 8, 1885, Eberlin). [Sweden: Åreskutan (Aug. 12, 1890).]

This species belongs to that group of the *Cassiope*

[1] Jungner, Klima und Blatt in der regio alpina. Flora, Bd. 79, 1894, p. 219.

which has neither furrows nor hollows. The leaf is shortly acicular, without protective devices except its small size. In agreement with the statement above given under *Cassiope tetragona*, the intercellular spaces are rather limited in size. But I am not prepared to say whether this is caused directly by the fact of the leaves having such slight external protective devices, or whether the chief reason must rather be found in the smallness of the leaf, which does not allow superabundant internal space.

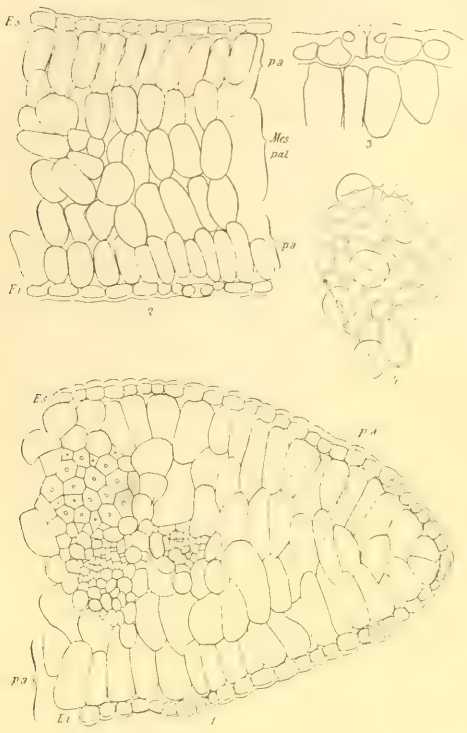

Fig. 22. *Cassiope hypnoides.*

The leaf. *1*, Transverse section. *2*, Longitudinal section not including the middle vein. *3*, Stoma. *4*, Epidermis with stomata. (Greenland, Aug. 1, 1892.) (H. E. P.)

The upper and lower epidermis are very much thickened by the presence of a cuticle and beneath it a cuticularized layer, and they have roundly angular lateral walls; only a few unicellular hairs of no importance occur along the margin of the leaf; the latter is usually somewhat flattened. The stomata, which are not confined to any particular area, project slightly or else occur on the level of the epidermis. The cells of the outer layer of the mesophyll, and partly those of the layer beneath are developed as palisade-cells and slant towards the apex when seen in longitudinal section. The central mesophyll has no large intercellular spaces and con-

sists more or less of elongated, irregular, parenchymatous cells which are branchless. The vascular bundle in the middle of the leaf is accompanied by a sclerenchymatous bundle which is large compared with the size of the leaf. The walls of the mesophyll are coloured slightly yellow by chlor-zinc-iodine.

The primary cortex of the stem consists of transparent cells without contents with a few which are thicker walled, and of trabeculæ like those in *Andromeda* and *Ledum*. It persists for several years. The secondary cortex consists of irregularly-angular corky cells. The annual rings are not distinct.

I have not examined the root (cf. Hesselman).

Andromeda polifolia L. (Figs. 23—24.)

Börgesen, 1895, pp. 234—235. Segerstedt, 1894, pp. 29—34. O. G. Petersen, 1901, p. 77. Schulz, 1888, pp. 254—255.

The specimens I have had for investigation are from the following localities: — West Greenland: Tiningnertok (62° 20', June 6); (Finmark) Bosekop (1885, E. W.); Tromsö (June 28, 1884, E. W.). [Denmark: bog at Herning (Aug. 5, 1887, E. W.); bog at Farum (Febr. 24, 1907, H. E. P.)]

The leaf. The outer walls of the epidermis are much thickened (6—8 μ in the specimens from Tiningnertok) by the presence of a thick cuticle and beneath it a cuticularized layer.

The upper epidermis has much-undulating lateral walls, and inner walls containing ligneous substances which are coloured red by phloroglucin-muriatic acid, a fact which is peculiar to *Andromeda* and does not occur in the other forms treated of in this paper. Hairs occur on the lower surface of the leaves in the Greenland specimens, but not on those in the Danish or Norwegian ones (Börgesen, l. c.); the above-mentioned hairs do not play any prominent part as protective structures, the layer of wax on the lower surface of the leaf which occurs

in all *Andromeda*-forms is more useful in that respect. Stomata occur only on the lower surface; they often project slightly. The inner sides of the guard-cells, as also the neighbouring cells of the epidermis are covered by cuticle. According to Lidforss chlorophyll grains occur in the upper epidermis. Palisade-cells occur in 2—3 layers about 30—40 μ in height

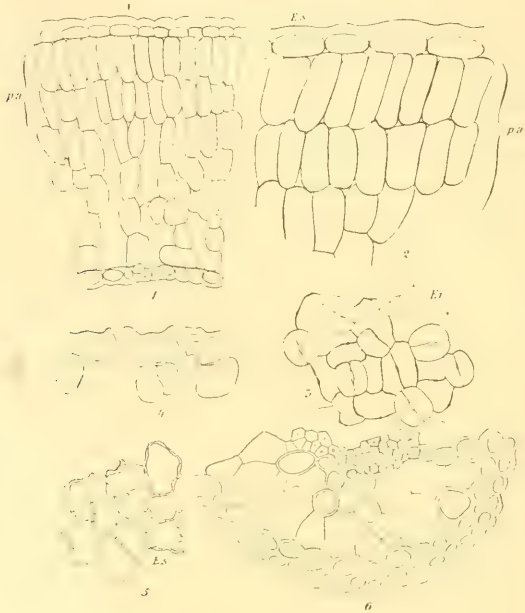

Fig. 23. *Andromeda polifolia.*

The leaf. *6*, shews the aqueous tissue and the thick-walled cells beneath the vascular bundle in the middle of the leaf. (*1—4*, Greenland: Tiningnertok, 62° 20′. *5*, Denmark: Sjælland.) (H. E. P.)

at the most, and slanting towards the apex. The spongy parenchyma is of about the same thickness as is the palisade-tissue and consists of non-branching cells which are usually transversely elongated across the leaf, making the latter somewhat isolateral, which circumstance harmonizes with the often somewhat erect position of the leaves. All the cells of the mesophyll are somewhat thick-walled. Tannin occurs abundantly

in all the cells, and is easily discernable in fresh material, but in spirit material it is seen only in the walls, which are found to be saturated with it, and some more than others (cf. Schulz). It is possible that the tannin is not distributed quite evenly.

Specimens from the bog at Farum (February, 1907) demonstrated very perfectly the Kraus winter-condition. The palisade-cells which are devoid of chlorophyll gave an exceptionally good reaction for tannin (cf. Warming, Beobachtungen über Pflanzen mit überwint. Laubblätter. Bot. Centralblatt, Bd. 16, p. 350).

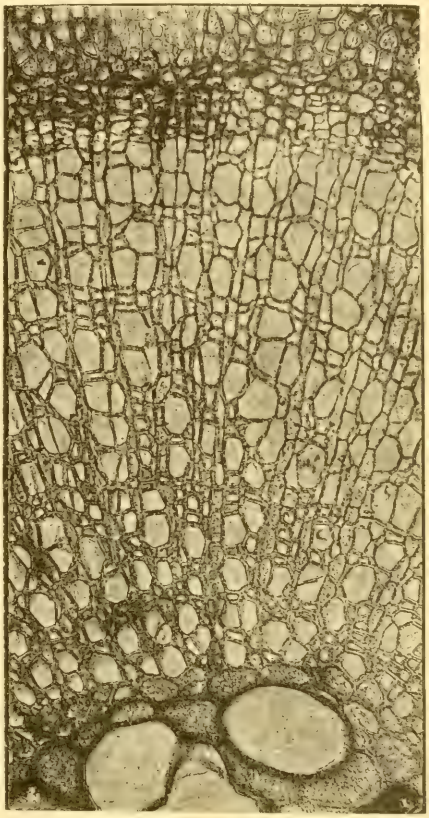

Fig. 24. *Andromeda polifolia.*
Transverse section of stem. × 180. (Tiningnertok.) (Phot.)

Below the central vascular bundle a tissue occurs consisting of very thin-walled cells (Fig. 23, 6), sometimes traversed by thick-walled cells which run from the ring of bast to the epidermis, a kind of aqueous-tissue. A similar tissue is also met with in *Ledum palustre*. Stereom is developed thickly around the vascular bundles. In regard to the structure of the leaves, excepting the difference already mentioned with reference to the development of hairs, which

occurs only in the Greenland specimens, I have not found any features of importance which serve to distinguish the Danish specimens from the Arctic ones.

The young stem has a primary cortex consisting of large, thin-walled cells, with a few thicker walled cells, and trabeculæ such as occur in the aqueous tissue below the central vascular bundle of the leaf; a uniformly cuticularized epidermis; and a large pith of similar structure to the cortex. The secondary cortex, which according to Segerstedt is developed on the lower part of the year's shoot, consists of angular cells which have become corky and contain starch.

In regard to the formation of annual rings, where the new annual ring begins, either a single tangential wall or several in succession may be observed. The single tangential wall or the outermost ones — in cases of several occurring in succession — collapse and form a continuous peripheral line. Where several tangential walls occur, the latter are within the line in question. I am not prepared to say whether these walls have been formed during spring or in late summer. I am inclined to believe that the latter is the most probable. Otherwise the annual rings do not shew any special differences in the development of the summer and autumn wood (Fig. 24) (O. G. Petersen, p. 77). As regards the structure of the stem I have not found any differences between the Danish and the Northern specimens in the material I have had at my disposal.

I have not examined the roots.

Lyonia calyculata (L.) Don. (Fig. 25.)

Cassandra calyculata (L.) Don.

O. G. Petersen, 1901, p. 76. Lidforss, 1907, p. 75.

Of *Lyonia* I have had only a very small quantity of material — a single sample from Finland — hence I have not been able to enter more fully into this species.

The leaf. The epidermis of the upper surface is smooth and fairly thick. The lateral walls of the cells are slightly undulating. The outer walls of the epidermis of the lower surface are not specially developed. Stomata are confined to the lower surface and have no protective devices. Hairs, of one kind only, viz. peltate, occur on both sides of the leaf. They agree most closely with the corresponding hairs in *Rhod.*

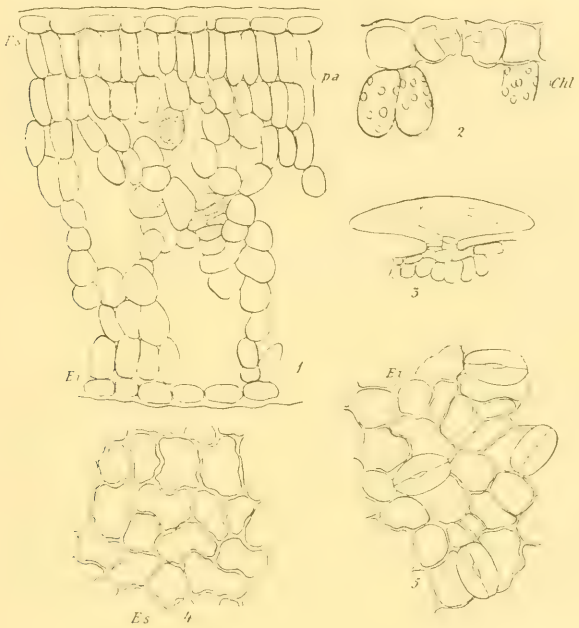

Fig. 25. *Lyonia calyculata.*
The leaf. *3*, Peltate hairs on the lower surface. Cf. note p. 81. (Finland.)

lapponicum, but on the lower surface they do not play any important part as a protective mechanism to the stomata, as is the case in *Rhod. lapponicum*. According to Lidforss, chlorophyll grains occur in the upper epidermis.

The palisade-tissue, which consists of 3—4 layers of fairly small cells, passes by easy stages into a lacunal central part, formed by trabeculæ of non-branching parenchymatous cells

with large intercellular spaces between the trabeculæ. This central part again merges gradually into a part which usually consists of two layers of cells, and which may be termed the palisade-tissue of the lower surface. Thus, there is a certain isolaterality in the leaf of *Lyonia* as in that of *Arctostaphylos Uva-ursi*, which species the present one resembles in regard to its mesophyll. Of these two species *Lyonia* has the more isolaterality which is connected with the fact that the leaves of this species are sometimes vertical.

Beneath the larger vascular bundles an ill-developed aqueous-tissue occurs, with trabeculæ of thick-walled cells of similar nature to those in *Ledum* and others. The stereom, which is of medium thickness, consists of libriform cells.

The limits of the annual rings were very indistinct in the material from the Botanic Garden in Kjøbenhavn (O. G. Petersen, p. 76).

Arctostaphylos Uva-ursi (L.) Spreng. (Figs. 26—27.)

Börgesen, 1895, pp. 234—235. Segerstedt, 1894, p. 34. O. G. Petersen, 1901, p. 74. Hesselman, 1900, p. 27.

The specimens I have had for investigation are from the following localities: — West Greenland: Ilivnek (July 1884, E.W.). Iceland: Thingvellir (June 8, 1884); Mossfellsheidi (June 14, 1895); loc. ign. (Jan. 6, 1894, H. Jónsson). Norway: Bosekop (July 7, 1885, E. W.); Sakkabani, 1000′ (1885, E. W.); Tronfjæld. [Denmark: wood at Hjortlund (July 21, 1892); Mölhede; Botanic Garden in Kjøbenhavn. Switzerland: St. Moritz.]

The leaf. The upper and lower epidermis are very much thickened (on an average as much as 16 μ) by the presence of a thick cuticle and beneath it a cuticularized layer. Lateral walls not undulating. Hairs occur only along the margin of the young leaf and are not of much importance. The stomata, which are confined to the lower surface, are somewhat sunk

on account of the outer walls of the epidermis being so much thickened. The cells of the spongy parenchyma below, and the inner part of the guard-cells, are suberised along the part of their walls which is towards the intercellular spaces. According to Lidforss chlorophyll grains occur both in the upper and in the lower epidermis.

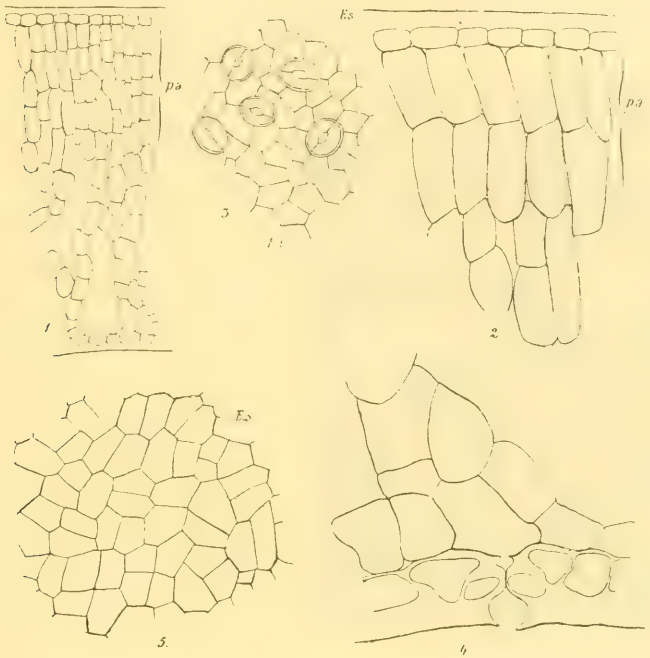

Fig. 26. *Arctostaphylos Uva-ursi.*

The leaf and its parts. Cf. note, p. 81. *1*, × about 100; *3*, *5*, × about 125; *2*, *4*, × about 250. (*1*, *2*, *4*, Finmark: Bosekop; *3*, Norway: Tronfjæld; *5*, Iceland.) (H. E. P.)

The palisade and the spongy parenchyma are distinctly differentiated, but the cells of the latter are in a great number of cases elongated in the same direction as that of the former, so that a kind of isolaterality is here found.

The layers of palisade-cells vary in number, as do the individual palisade-cells in regard to height.

In specimens from Bosekop, Tronfjæld and Sakkabani the

layers are from 4 to 5 in number; the cells measuring 67 μ by 120 μ in height (highest measure).

In specimens from Hjortlund, Mölhede, and the Botanic Garden in Kjøbenhavn the layers are from 2 to 3 in number; the cells measuring about 67 μ in height.

In the specimens from St. Moritz the palisade-tissue was found to be of a still greater thickness, but perhaps we are here dealing with an Alpine or Subalpine species; and as it is contrary to what is usually found that the thickness of the palisade-tissues should increase the farther we advanced northwards, I do not attach any great importance to the facts mentioned above, the material being too scanty for any reliable conclusions to be based upon it.

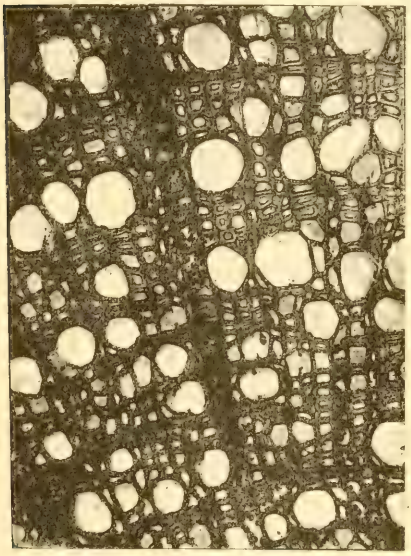

Fig. 27. *Arctostaphylos Uva-ursi.* Transverse section of stem. × 180. (Denmark: Mölhede.) (Phot.)

The upper layer of the palisade-cells slants somewhat towards the apex.

Large intercellular spaces occur in the spongy parenchyma, which is formed by cells which branch but slightly and are transversely elongated. Tannin occurs in all the elements of the leaf.

Stereom is very slightly developed, in correlation with the much-thickened epidermis.

The stem. The primary outer cortex (cf. Segerstedt) consists of a regular, much cuticularized epidermis without stomata, beneath which is a tissue consisting of fairly homogeneous,

rounded cells without intercellular spaces. In the innermost layer isolated bast-cells occur. The secondary cortex, which according to Segerstedt is produced on branches 3—5 years of age, does not renew the epidermis as is the case in *Arct. alpina*. There are typical annual rings, and the spring and summer wood are distinctly differentiated. Now and then a tendency may be traced towards the formation of irregular, ill-defined annual rings, a fact which is often met with in the other *Ericaceæ*, *Rhodoraceæ* and *Vaccinaceæ* treated in the present paper.

In the root I have not observed endotrophic hyphæ (cf. Hesselman).

Except the difference in regard to the palisade-cells I am not aware of having observed any other points in which the specimens from other countries differed from the Danish individuals.

Arctostaphylos alpina (L.) Spreng. (Fig. 28.)

Börgesen, 1895, pp. 236—237. O. G. Petersen, 1901, p. 75. Ambronn, 1890, p. 70.

I have had specimens for investigation from the following localities: — East Greenland: Hekla Havn (N. Hartz); Danmarks Ö (April 10, 1892, N. Hartz). Norway: (Finmark) Tromsö at Flöjfjæld (July 24 and 27, 1885, E. W.). Sweden: Jämtland (July, E. W.). Denmark: diff. localities.

The leaf being deciduous, it naturally differs somewhat in structure from that of the previous plant. Structures which tend to check excessive transpiration and which are especially necessary to protect plants against the dryness of the winter's cold, do not occur. The present species differs from the above in regard to the assimilatory tissue also, which is in itself peculiar as evergreen leaves do not assimilate very much during winter; in short we are here dealing with quite a different type.

The upper and lower epidermis are thin-walled throughout and have no thick cuticle or cuticularized layer. The outer walls are, however, coloured yellow by chlor-zinc-iodine. The

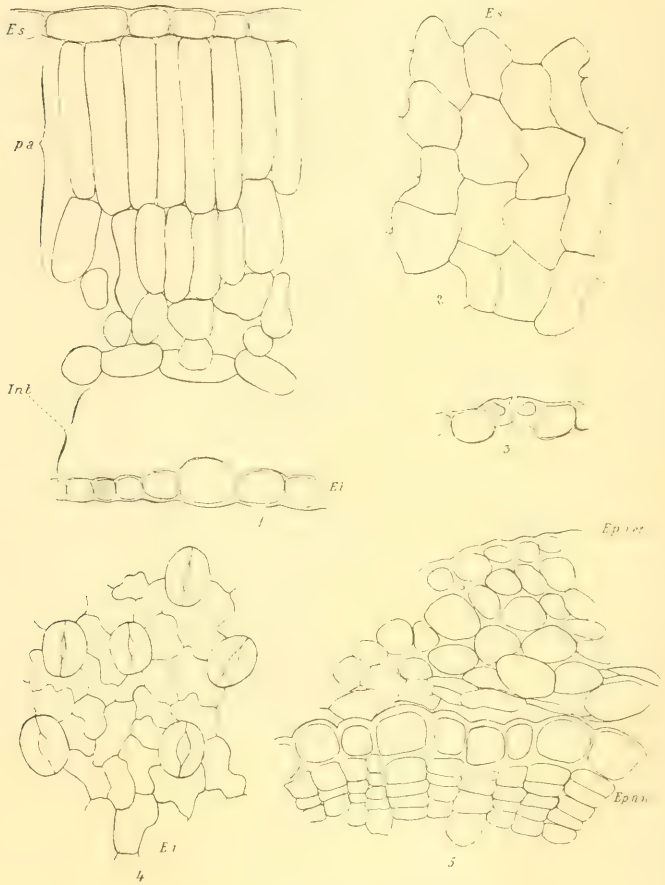

Fig. 28. *Arctostaphylos alpina.*

1—4, The leaf. *Ei*, The large air-cavities formed by the epidermis of the lower surface having separated from the mesophyll; some of the large cells of this epidermis may also be seen. *5*, shews how the new epidermis of the stem is formed. (Finmark: Tromsö: Jan. 5.) (H. E. P.)

cells of the upper epidermis have slightly undulating lateral walls while those of the lower are strongly undulating. Hairs are absent. The stomata are confined to the lower surface and

project slightly. Besides the guard-cells the epidermis of the lower surface consists partly of small and partly of large cells; the latter, as it appears, function as a kind of aqueous tissue, such as often occurs in the neighbourhood of vascular bundles. According to Lidforss chlorophyll grains occur both in the upper and in the lower epidermis.

The palisade-cells occur in a single layer only, but are long (about 80 μ), nearly as long as the spongy parenchyma, and seen in longitudinal section to be placed somewhat obliquely, especially in the neighbourhood of the vascular bundles. The cells of the spongy parenchyma, which are but slightly branched, are usually elongated parallel to the surface of the leaf. Large intercellular spaces occur; in connection with the latter it may be mentioned that the epidermis of the lower surface easily separates from the spongy parenchyma, often forming unusually large air-cavities.

The stem. The epidermis and the cortex of the young stem are similar to those of *A. Uva-ursi*. When the secondary cortex arises, and the formation of cork begins at the boundary between the primary and the secondary cortex, a layer, which has already previously been distinctly differentiated, is developed as a new epidermis which, as far as I can judge, persists for a shorter or longer time (several years) (Fig. 28, 5). But when once this new epidermis falls off it is not renewed, and then the external investment of the stem is formed by the cork-layer itself, which develops early (see Fig. 28,5) and exhibits no points of interest. The annual rings in the woody part resemble those in *A. Uva-ursi*; usually they are distinct, with a more or less marked difference between the autumn and spring wood, but sometimes these are somewhat indistinguishable. Normally, vessels are formed in the spring wood and tracheids in the autumn wood.

I have not examined the roots.

Vaccinium Oxycoccos L. et var. *microcarpum* (Figs. 29—31.)

Syn. *Oxycoccos palustris* Pers.

Segerstedt, p. 27. O. G. Petersen, p. 81. Hesselman, 1900, p. 27.

The specimens I have had for investigation are from the following localities: — West Greenland: Godthaab (1895). Finmark: Alten (July 7, 1885). Norway: (Finmark) Bosekop; (Dovre) Vaarstien (July 13, 1887). Denmark: bog at Lyngby and Farum: (Jutland) Bjærget in Thy.

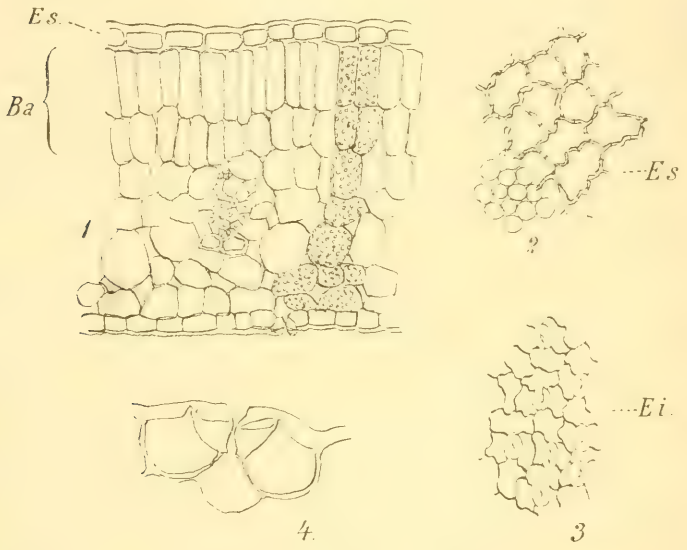

Fig. 29. *Vaccinium Oxycoccos.*
The leaf. Cf. note, p. 81. (Denmark: Lyngby bog.) (E. Warming.)

The leaf has no special protective devices as, for example, hairs; a wax-layer occurs only upon the lower surface.

Both the upper and lower epidermis are very much thickened with cuticle and beneath that a cuticularized layer; their cells have wavy lateral walls and contain chlorophyll grains. The stomata, which are confined to the lower surface, are on a level with the epidermis and occur in considerable numbers relatively to the size of the leaf. This should probably be connected

partly with the small number of leaves and partly with the often great length of the stem which requires an abundant supply of air. Further, it must also be a fact of importance in this connection that the leaves occur only slightly above the level of the soil and in an atmosphere fairly rich in carbonic acid; this increases the necessity for oxygen. Upon the inner side of the guard-cells and upon the adjacent cells a cuticularized outer layer may be seen.

The palisade-tissue consists of 1—2 layers, and the cells are at most 80 μ in length. On comparing Danish and northern

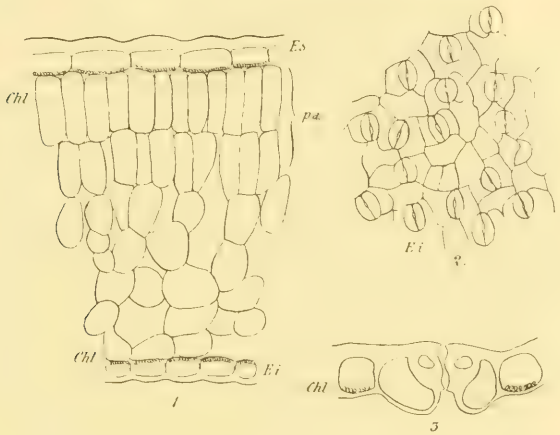

Fig. 30. *Vaccinium Oxycoccos.*
The leaf. Cf. note p. 81. (Finmark: Bosekop.) (H.E.P.)

specimens I have not found any special differences, except perhaps that the lower layer of palisade-cells is better developed in the northern specimens.

The cells of the spongy tissue are not much branched and form lamellæ which lie somewhat transversely across the leaf a circumstance which harmonises well with the often vertical position of the leaf. The cells of the mesophyll are fairly thick-walled. No aqueous tissue occurs, but a considerable amount of stereom. The Kraus winter-condition was observed on Febr. 24, 1907 (Farum bog), but not on March 22, 1907 (Lyngby

bog), nor on Novbr. 11, 1906 (Ruder Hegn (wood)). In the upper palisade-cells a red cell-sap occurs during winter, and then the contents of these cells always give a good reaction for tannin. But in the leaf tannin also occurs in the other cells of the

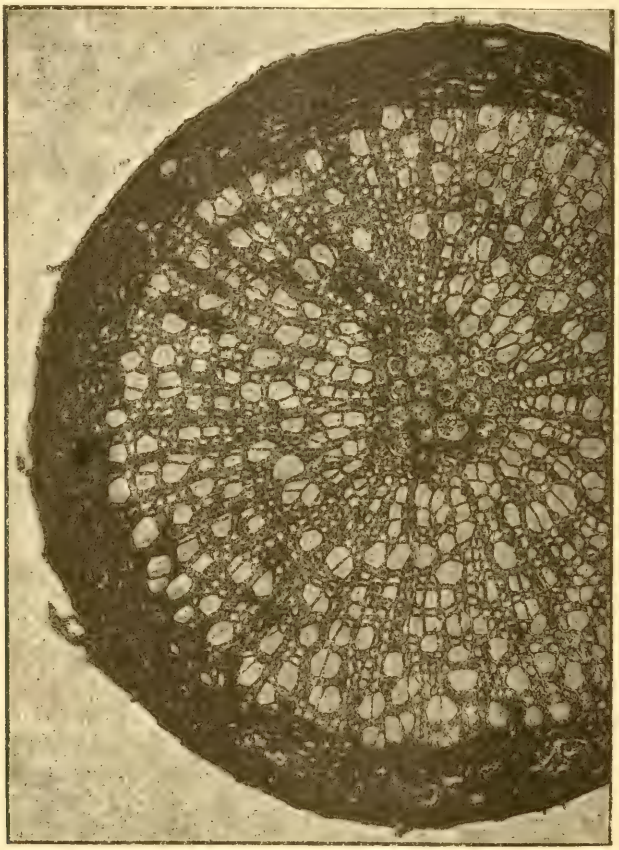

Fig. 31. *Vaccinium Oxycoccos.*
Transverse section of stem (Denmark). × 180. (Phot.)

mesophyll. There is scarcely any other difference between the Danish and the northern specimens than the one indicated above.

The stem. The primary cortex consists of a fairly compact tissue of parenchymatous cells with a rather slightly de-

veloped epidermis. The secondary cortex is found early in June and consists of regularly arranged cork-cells (Segerstedt). The limit between the yearly rings of growth in the wood is not sharply defined, neither is there any difference between the spring and summer (or autumn) wood.

The roots have not been investigated (cf. Hesselman).

Vaccinium Vitis-idæa L. (forma pumila Hornemann). (Figs. 32—33.)

Segerstedt, p. 26. O. G. Petersen, p. 81. Tedin, 1892, p. 74. Maury, 1887, p. 108. Hesselman 1900, p. 27.

I have had specimens for investigation from the following localities: — West Greenland: Isortok (June 8, Kornerup); Kristianshaab (July 26, 1884, Hartz 1890). Norway: Bosekop (July 9, 1885, E. W.); Kåfjord (July 10 and 15, E. W.); Tromsö (July 13, 1884, E. W.); (Dovre) Kongsvold (July 13, 1887, E. W.).

The leaf has no special protective hairs.

The upper and lower epidermis have much-thickened outer walls, with cuticle and beneath that a cuticularized layer, and slightly undulating, thickened lateral walls with numerous pores. Chlorophyll grains occur in the lower epidermis. In small hollows on the lower surface multicellular (glandular) hairs occur which are, however, of no importance as protective devices. The stomata are confined to the lower surface and do not project. The outermost layer of the inner

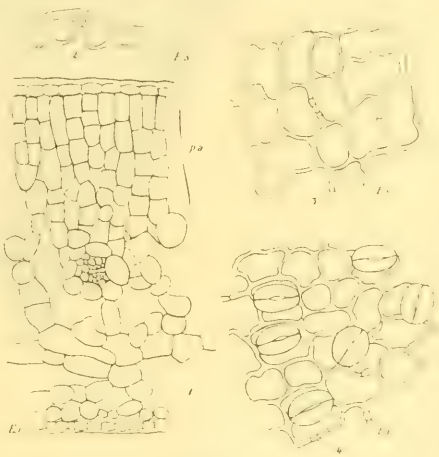

Fig. 32. *Vaccinium Vitis-idæa.* The leaf. Cf. note p. 81. (Greenland.) (H. E. P.)

walls of the guard-cells and of the neighbouring cells is cuticularized. The palisade-cells occur in several layers and are about 50 μ in length. In regard to the palisade-tissue the Subarctic and the Arctic specimens do not appear to be in any way inferior to the Danish specimens (of the typical species).

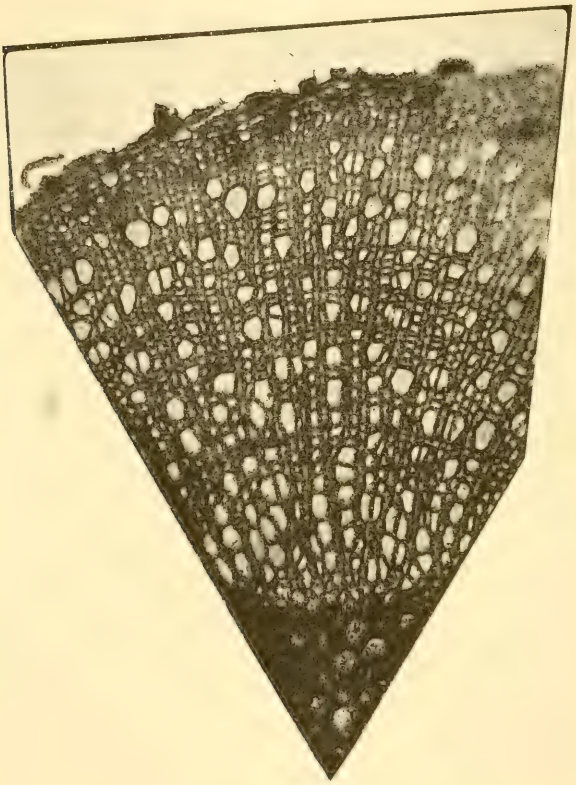

Fig. 33. *Vaccinium Vitis-idæa.*
Transverse section of stem. × 180. (Greenland.) (Phot.)

In shade-forms (which, as is well-known, always accompany light-forms), Subarctic specimens of which, however, I have not had for investigation, the elements of the leaf are naturally reduced in size (especially the palisade-tissue). The spongy parenchyma is not much branched and has very large intercellular spaces of

about the same size as those in the palisade-tissue. No aqueous tissue occurs, nor is the stereom especially well-developed. In the material I had for investigation no difference could be observed between the Danish, the Subarctic and the Arctic specimens. But here, as was the case with regard to the other species, the material was too scanty to be useful for the investigations in question. The specimens from Furca Pass, Switzerland (Aug. 1904; H. E. P.), did not shew any differences of importance.

The stem. According to Tedin (1892, p. 74) the primary cortex consists partly of transparent, thin-walled cells containing water and partly of thick-walled cells which contain chlorophyll and occur partly in trabeculæ and partly in groups (cf. e. g. *Ledum*). It persists for about three years. The secondary cortex, according to Segerstedt, consists of an ordinary cork-tissue.

The spring wood is differentiated from that of the summer (or autumn); but the limits of the annual rings are not always sharply defined. According to Simon (1902) the cause of the distinctness of the annual rings in *Vac. Vitis-idæa*, and of the differentiation of the wood of the different seasons as mentioned above, will be found in the fact that evergreen forms require more stereom, while the deciduous forms need relatively more "Speichergewebe;" but this is scarcely to be regarded as a universal rule (cf. *Ledum, Rhododendron*, etc.).

The roots I have had for examination from Hovmose in Gadevang at Frederiksborg shewed both endotrophic and ectotrophic mycorhiza.

Vaccinium uliginosum L. (with f. **microphyllum** Lge.)

(Figs. 34—37.)

Börgesen, 1895, pp. 236—237. Segerstedt, p. 25. Ambronn, 1890, p. 71. O. G. Petersen, 1901, p. 81. Hesselman, 1900, p. 27. Maury, 1887, p. 105.

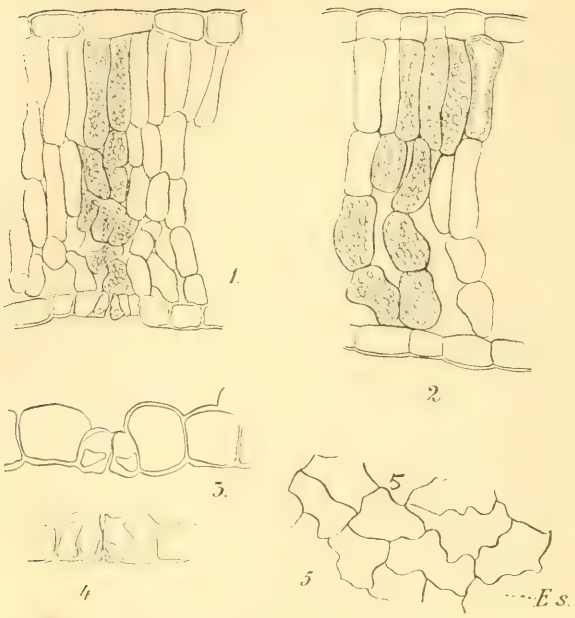

Fig. 34. *Vaccinium uliginosum.*

The leaf. *1*, *2*, Transverse section. *3*, *4*, Stomata. *5*, The epidermis of the upper surface. (West Greenland.) (E. Warming.)

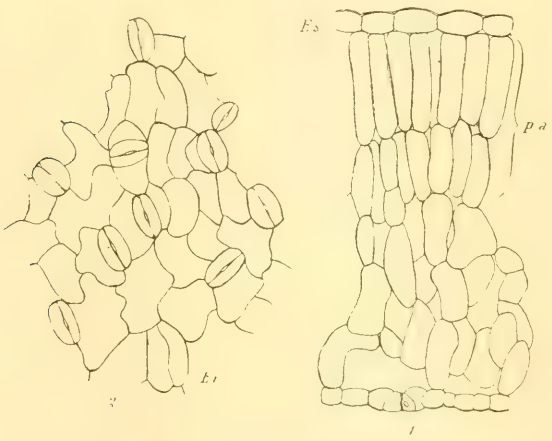

Fig. 35. *Vaccinium uliginosum.*

1, Transverse section, and *2*, epidermis of the lower surface, (Greenland: Upernivik.) (H. E. P.)

I have had specimens for investigation from the following localities: — West Greenland: Buxefjord (Aug. 17, 1884, E. W.); Sukkertoppen (Aug. 16, 1884, E. W.); Upernivik (July 13, 1886 and July 11, 1887, Ryder); Upernivik's Ö (July 10, 1886): tent 8 (July 13, 1886, Ryder); tent 16 (July 30, 1887, Ryder): loc. ign.

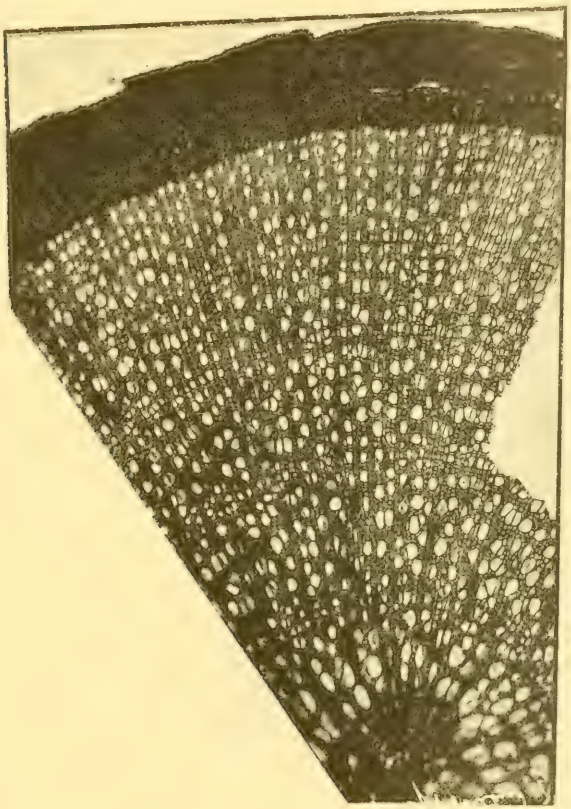

Fig. 36. *Vaccinium uliginosum.*
Transverse section of stem. × 60. (Greenland.) (Phot.)

(June 6, 1874, Kornerup). East Greenland: Hekla Havn (Nov. 4, 1891, N. Hartz). Norway: (Finmark) Tromsö (June 28, 1884, E. W.), and loc. ign. (July 4, 1884, E. W.). Iceland: Godaland (June 23, 1886, Feddersen). Denmark: diff. localities.

The leaf is of the same type as that of *Arctostaphylos*

alpina; it is deciduous, hairs are absent, and there is only a waxy covering.

The upper and lower epidermis are only slightly thickened and have no specially cuticularized layer beneath the cuticle; the lateral walls are slightly undulating. The stomata are confined to the lower surface and do not project.

The palisade-tissue consists of 1—2 layers of cells, with a height of as much as 100 μ, and it is somewhat unequally developed, the lower layer being less developed when the upper consists of long cells. The cells of the spongy parenchyma are more elongated in the vertical than in the horizontal direction and often branch but slightly; the intercellular spaces are large. The whole of the mesophyll is loosely built. In the material at my disposal I have not observed any difference between Danish, Subarctic, and Arctic specimens.

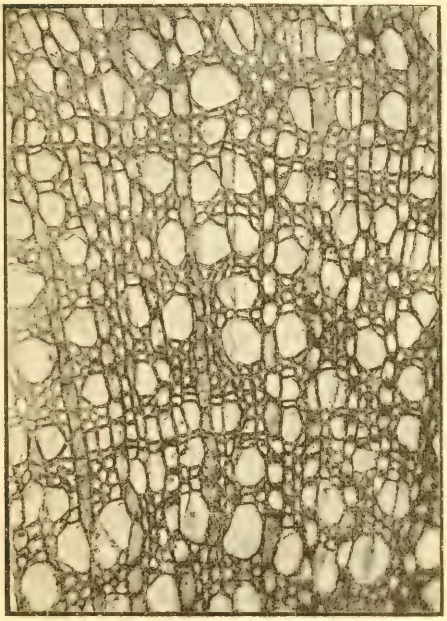

Fig. 37. *Vaccinium uliginosum.*
Transverse section of stem × 180. (Phot.)

The stem. The primary cortex consists, according to Segerstedt, "of a few layers of cells of which the outermost have scanty chlorophyll-contents with walls thicker than those of the inner, which are loosely connected and the contents of which are colourless." The epidermis

is not especially thickened. In the most internal cortex a few bast-cells occur.

There is only a slight trace, or none at all, of difference between the spring and autumn wood. As may be seen in Fig. 37 annual rings evidently occur, but it is not always easy to distinguish their boundaries.

The roots have not been investigated (Hesselman, p. 27).

Vaccinium Myrtillus L. (Figs. 38—39.)

Fig. 38. *Vaccinium Myrtillus.*

The leaf. Cf. note p. 81. *6*, Stoma of the stem. *5*, Hair from the margin of the leaf. (*1*, Tromsö; *2*, *4*, Stockholm.) (H. E. P.)

Segerstedt, p. 20. O. G. Petersen, 1901, p. 80. Maury, 1887, p. 105. Woodhead, 1904—06, pp. 387—391.

I have had specimens for investigation from the following localities: — Norway: (Finmark) Tromsö (June 6, 1884, E. W.); (Dovre) Vaarstien (July 15, 1887, E. W.); (Dovre) Kongsvold (July, 1887, E. W.). Sweden: Stockholm (1888, E. W.). Denmark: diff. localities.

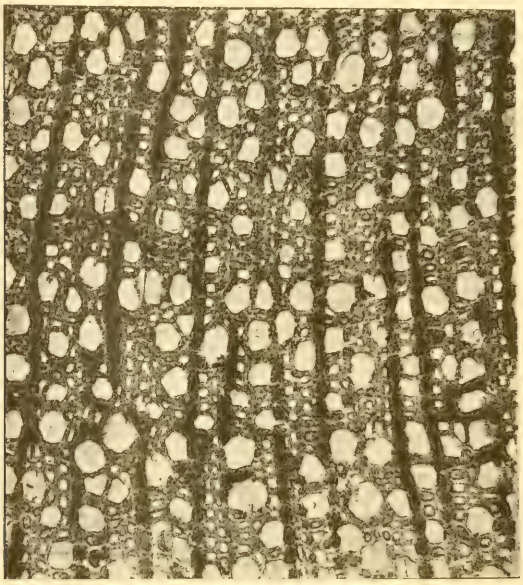

Fig. 39. *Vaccinium Myrtillus.*
Transverse section of stem. (Denmark: Ruder Hegn (wood).) × 180. (Phot.)

The leaf is of the same type, both morphologically and anatomically, as that of the preceding and that of *Arct. alpina*. No special protective hairs occur, nor is a wax-layer present.

The upper and lower epidermis have very thin outer walls and no thick cuticle nor cuticularised layer. The lateral walls are undulating. At the margin of the leaf and along its larger veins the leaf-tissue appears to be prolonged into characteristic

multicellular glandular hairs (Fig. 39, 5) (cf. Woodhead) which are probably of importance as protective devices in the bud-condition only, if indeed they have any importance in the above connection. Besides these, ordinary unicellular hairs occur in the same situation. The palisade-cells are of one layer only, about 35 μ in height, and loosely connected. The spongy parenchyma is few-layered and has large intercellular spaces. Aqueous tissue and stereom are absent. The whole of the leaf is loosely built.

The stem. I shall not enter more fully into the structure of the stem, but shall only refer the reader to Segerstedt and Simon. There is no great difference between the spring and summer (or autumn) wood, and the limits between the different annual rings are not very distinct.

I have not examined the roots.

Summary of the *Ericaceæ*.

In the present summary I shall briefly compare the chief results arrived at from the special consideration of the biological anatomy of the individual species. I shall begin by comparing the species with each other in regard to protection against the danger of excessive transpiration as indicated by the structure of the leaf; and in regard to the adaptation to light as expressed in the structure of the palisade-tissue; comparing in fact, the separate types of leaf-structure in their relation to external factors. The results thereby arrived at will be viewed in the light of the geographical distribution of each species. In the comparison of species according to the developmental stage reached by their leaf-structure in relation to the climate, they should, of course, occur in the same habitats or at least

in localities which are identical when viewed from a physiological point of view.

Lastly the species within each morphological type should be compared with each other. Quite a distinct matter is the mutual comparison of the types, but into this I shall not enter in the present summary.

In regard to the localities in which occur the species with which we are here dealing, I have not any exhaustive knowledge of their nature, but I feel able to state that on the whole it is scarcely possible that any differences of importance can exist. With respect to all the evergreen forms, the winter and early spring is the time which decides the degree of protection needed against excessive transpiration, but during winter and early spring the nature of the localities is hardly of any consequence, the soil in all cases being entirely frozen; but possibly a more or less thick covering of snow may be of importance.

Hartz writes in Östgrönlands Vegetationsforhold[1] that *Cassiope tetragona* and *Rhododendron lapponicum* are often found in places bare of snow, but only the former may be said to thrive well there. The other *Ericaceæ* he mentions in the paper in question appear mostly to be covered by snow. It is doubtless customary for all of them to be, as a rule, covered by snow. But if it be now customary for the *Ericaceæ*, and, on the whole, the dwarf shrubs of moors and rocky flats, to be covered by snow during winter, we may ask of what importance are the xerophytic structures. In regard to this I shall first refer to what Warming says in Grönlands Vegetation. He writes (p. 121) that "it now and then may happen, and happens everywhere in the Polar regions, that large areas remain bare of snow all through the winter or are very early laid bare of snow, consequently, it is evident that it is especially those leaves that live more than a year that must be

[1] Meddelelser om Grönland, Vol. 18, p. 182.

protected against excessive transpiration." Kolderup Rosenvinge writes in Det sydlige Grönlands Vegetation[1] "The strong winds prevailing in the mountains (Föhnen) will be especially dangerous to plants during winter when it either melts the snow or causes it to evaporate largely." The fact that the plants are thus casually laid bare during winter, as also the melting of the snow in early spring, are both doubtless very dangerous, and sufficiently account for the formation of organs that tend to check transpiration. In accordance with this, Lidforss writes in his paper on the evergreen flora (1907) that it is especially the frozen soil during spring that is of importance in the above-mentioned respect. The spring is doubtless otherwise a very damp season in the Arctic regions. Thus the snow-covering hardly plays any prominent part in regard to those structures of the *Ericaceæ* which we are here considering. With regard to the two above-mentioned species, *Rhodod. lapp.* and *Cassiope tetragona*, we are probably not justified in connecting the fact of their occurrence in exposed localities with their structure except that such occurrence is due to the fact of their structure being especially xerophytic. It should be remembered that they occur also in less exposed localities, and strictly speaking, most frequently there. On the whole, there is hardly any particular feature in the nature of the habitats of the *Ericaceæ* with which we are here dealing, which should cause the appearance of different degrees in the adaptations for withstanding drought. With regard to light they all stand on an equality as far as I can see.

The species belonging to the deciduous group, which may come into consideration in this connection (strictly speaking only *Vaccinium uliginosum* and *Arctostaphylos*, as *Vacc. Myrtillus* is not quite Arctic) are doubtless similarly situated as regards the external conditions.

[1] Meddelelser om Grönland, Vol. 15, p. 108.

I may add that I am well aware that the views given above are in many points open to criticism.

The Leaf.

Among the forms with broad leaves which persist through the winter *Rhododendron lapponicum* is doubtless the one that is specially Arctic, and one of the oldest forms of this region: consequently, it may well be the first to be dealt with. Here we find a thick epidermis on both surfaces; a well-developed covering of peltate hairs; stomata especially well-protected; several layers of small palisade-cells; and a slightly branching spongy parenchyma arranged in lamellæ around the large intercellular spaces. With regard to the last-named feature it may be mentioned that it would be quite indefensible to connect them at all with Arctic conditions such as, for example, the great dampness of air in these regions. According to Lalanne, leaves which may be several years' old, provided they are not too small, have large intercellular spaces. This feature is not dependent upon any particular climate, but should rather be connected with the thickness of the epidermis, which affords good protection against the danger of excessive transpiration: or better still, the spaces may be rendered necessary in the present instance, because the stiff, coriaceous leaves cannot be stirred so freely by the wind as are deciduous leaves.

Trying next to find a species which is as well protected as *Rhododendron*, we come to *Ledum*. This is a very common species in the Arctic regions, but it has in addition a much more southerly distribution, in districts with a continental climate, and consequently, a severe winter. It is scarcely as typically Arctic as *Rhododendron*, neither is it as old-established in the region as the latter. Nevertheless it is justifiable to surmise that its structure reflects to some extent the Arctic climate. The stomata are perhaps not so well protected as those in *Rhododendron*, but on the other hand we have here

more definite aqueous tissue. The palisade-cells are somewhat longer than in *Rhododendron*, particularly in the decidedly Arctic form *L. decumbens*. Here we have (in *Rhododendron* and *Ledum*), without going deeper into the matter, two distinct kinds of palisade-tissue; which shews that in the Arctic moorland plants the height of the palisade-cells is practically immaterial, so that with regard to this feature the plants may retain unmodified their natural condition. As regards *Ledum*, its southern distribution may possibly be connected with the height of its palisade-cells. Both the species are well furnished with protective devices against excessive transpiration, a fact which is of ordinary occurrence in the Arctic moorland plants.

The next five forms which come under consideration, *Arctostaphylos Uva-ursi*, *Andromeda*, *Lyonia calyculata*, *Vaccinium Vitis-idæa* and *Oxycoccos* can scarcely be said to have their chief distribution in the Arctic regions. Among them, *Lyonia calyculata* and *Arctostaphylos Uva-ursi* extend, perhaps, farthest north. In connection with this, these two species, which also most resemble each other in points of leaf-anatomy, are best protected against the danger of excessive transpiration — *Lyonia* by its hairs, and *Arctostaphylos* by the thick outer walls of its epidermis. These two species have moreover the small-celled palisade-tissue characteristic of *Rhododendron*; among the less protected species this tissue occurs in *Vaccinium Vitis-idæa* only. This species has about an equal degree of protection as *Vaccinium Oxycoccos* and *Andromeda*, which two have wax on the lower surface of their leaves. With regard to protection against the danger of excessive transpiration, all the five above-mentioned species rank low compared with *Rhododendron* and *Ledum*; the reason for this may perhaps be found either in their special nature, or, in their former or present position relative to the Arctic regions. As regards the three latter, the Arctic part of their distribution is more

peripheral than that of the two former. The palisade-cells in *Vaccinium Oxycoccos* and *Andromeda* are long and occur in layers which are fewer and of greater thickness than in *Ledum*. And they bear further testimony to the fact that in the Arctic regions the palisade-tissue is independent of light and of drought. The want of protection exhibited in *Vacc. Vitis-idæa* and *Andromeda* appears to have resulted in the cells of the mesophyll becoming fairly thick-walled. The development of cuticle on the inner walls of the guard-cells and adjacent parts is common to all the forms upon which hairs are not developed.

All the forms with furrowed and acicular leaves have in their mere outline, and also in the position of their stomata, a special advantage over the broad-leaved forms. *Loiseleuria* is least protected in regard to its outline. But nevertheless the leaves of this form may be said to be well protected by a thick epidermis, by mucilaginous walls, and by dense hairiness. The palisade-cells are of about medium height. It will excite no surprise to learn that *Loiseleuria* is common in Arctic regions.

Phyllodoce somewhat resembles *Loiseleuria* in structure, but is possibly more xerophytic than the latter. The palisade-cells are here also of medium size as are those in *Ledum*. *Phyllodoce* is hardly so decidedly Arctic as is *Loiseleuria*.

Cassiope hypnoides and *Cassiope tetragona*, especially the latter, must be regarded as those which shew most adaptation. I shall not here repeat their characteristics, but it will suffice to point out that they are decidedly Arctic (*Cass. hypn.* occurs in the Southern Alpine regions), and that the palisade-tissue consists of cells which are, if anything, somewhat small. As is the case with *Ledum* and with *Rhododendron* among the broad-leaved species, so also here, the protectional devices against the danger of excessive transpiration are highly developed. These two forms have probably originally been developed under Arctic (Alpine) conditions. I am not able to decide what

is the age-relationship, from a purely Arctic (Alpine) point of view, which exists between the four above-mentioned species, but I am inclined to believe that the species of *Cassiope* are the oldest in that respect.

The leaves of the deciduous forms scarcely suggest an Arctic climate. They are all built more compactly than are the leaves in the forms especially mentioned by Börgesen (1895); but then it must be remembered that they occur also in moorland soil or at any rate in sour, peaty soil. Of these forms only *Vacc. uliginosum* is common in the Arctic regions. Anatomically it hardly differs from the southern forms. Judging especially from the fact of *Arctostaphylos alpina* having larger intercellular spaces it is doubtless less xerophytic than is *Vacc. uliginosum*. *Vacc. Myrtillus* is scarcely sufficiently old-established in the Arctic regions to be referred to the Arctic Flora.

Among the cases in which I have investigated the leaves of southern specimens, only rarely have I been able to prove that a lessening of the palisade-tissue accompanies further advance southwards into the lowlands. But then it must be remembered that the material has not in any way been complete. In regard to the slight difference observed in the xerophytic structure of the North-European and of the Arctic individuals of the same species, this may possibly — only possibly — be due to the fact that winter-time, the most dangerous time of the year, the time when evergreen leaves need the greatest protection, does not in many points differ greatly in the localities in question.

All the species described in the present paper have tannin in their leaves; most likely it is a family characteristic which is useful to them in the Arctic regions. In some Danish and a few Arctic specimens I have seen the plasma and the chlorophyll-contents of the evergreen leaves in the winter condition

described first by G. Kraus, but since then very little noticed.[1] In all the evergreen forms these contents are doubtless considerably contracted for a shorter or longer period during the winter, either in the palisade-cells only, or also in a part of the cells of the mesophyll. With regard to the individual cases in which this condition has been demonstrated, reference should be made to the particular section.

The Stem.

In the cortex of the stem of *Ledum, Andromeda, Cassiope hypnoides, Phyllodoce* and *Loiseleuria* occur transparent aqueous-tissue cells, among which are scattered a few thicker-walled cells with contents, or else lamellæ of the above cells occur: the tissue in question occurs also below the central vascular bundle in the leaf of *Ledum* and *Andromeda*. The protection of the stem against the danger of excessive transpiration does not on the whole present any features, other than those mentioned above, which can be serviceable for classifying the individual forms. The fact that the cortex has often no decided xerophytic character is doubtless occasioned either by the compact and low growth of the plant or by the circumstance that the old parts of the cortex, though more or less separated, yet adhere for a long time to the stem. The differences with regard to the formation of the annual rings which have been pointed out above, as also the often very slight distinction between the different elements of the wood—both these, and especially the latter, are no doubt systematic characters. In the southern specimens of certain species that extend southwards, we find the elements of the wood as slightly differentiated as those in the northern specimens — stereom is especially ill-developed, — a circumstance which must bring us to abandon

[1] Cf. Ritter v. Guttenberg: Anatom. phys. Untersuchungen über das immergrüne Laubblatt der Mediterranflora. Engl. bot. Jahrb. Bd. 38, 1907, p. 410.

the theory that the short period of growth in the Arctic regions is the cause of this slight differentiation. But in spite of this it does not follow that the short period of growth is of no importance whatever in this connection; it is undoubtedly instrumental in lessening the difference between the different elements of the wood; but as yet there hardly exists any accurate data on this point. In some cases other circumstances, such as slight need of stereom (in the case of prostrate stems), are doubtless of importance.

Lastly if, with reference to what I have indicated in the introductory lines, I am to point out the species which are most in conformity with the Arctic climate, then among the evergreen species it must be *Rhododendron lapponicum*, and to a certain extent *Ledum* and *Cassiope tetragona* (*Cassiope hypnoides* also in a measure) and among the deciduous species *Vaccinium uliginosum*.

It is only the structure of the leaves which is of importance in this connection, the stem and the root not shewing any special points of interest in this respect. Among the evergreen species, the greatest progress has doubtless been made by *Rhododendron lapponicum* and *Cassiope tetragona* — both true Arctic species which have most probably been long-established in the region in question, — and only such evergreen species as have, each in its own way, assumed the degree of protection attained by these two, will be able to continue to exist in the Arctic climate. Among the deciduous species such decided differences are not to be found as occur among the evergreens.

Postscript.

When working upon the *Pirolaceæ* W. Rommel's paper Anatomische Untersuchungen über die Gruppen der Piroleæ und Clethraceæ, Heidelberg, 1898, escaped my attention; in it the anatomy of the *Pirolaceæ* is treated of, especially that of the stem and root. That paper would not, however, have influenced my treatment of the species in question, as the exclusively biological point of view which I have adopted in the present paper required an independent, fresh description. But Rommel's paper should be mentioned here. For the sake of uniformity I give here the respective pages in Rommel's paper: — *Pir. rotundifolia*, p. 19, *Pir. minor*, p. 11, *Pir. secunda*, p. 22, *Chimophila umbellata*, p. 28.

30—6—1908.

2.

Diapensiaceae.

Diapensia lapponica L.

By

Henning Eiler Petersen.

1908.

Introduction.

In this short paper, following the method I adopted in my paper Ericineæ (Pirolaceæ, Ericaceæ) 2. The biological anatomy of the leaves and of the stems,[1] I intend pointing out such characters in *Diapensia lapponica* as are more particularly connected with the climatic factors. As this species has been very exhaustively described in the literature which deals with it, there have been only a few new data for me to record.

I have had a fairly large quantity of material at my disposal from West and East Greenland and from Finmark, which has enabled me to verify the different statements.

A List of the chief Literature: —

Borgesen, F., 1895: Bidrag til Kundskaben om arktiske Planters Bladbygning. (Botanisk Tidsskrift, Bd. 19.)

Cleve, A., 1901: Zum Pflanzenleben in Nordschwedischen Hochgebirgen. (Bihang till kgl. sv. Vet. Ak. Handl., Bd. 26, Afd. III, 15, Stockholm.)

Grevel, W., 1897: Anatomische Untersuchungen über die Familie der Diapensiaceae. (Bot. Centralblatt, Bd. 69.)

Hesselman, H., 1900: Om Mykorrhizabildningar hos arktiska växter. (Bihang till kgl. sv. Vet. Ak. Handl., Bd. 26, Afd. III, 2, Stockholm.)

Lindman, C. A. M., 1887: Bidrag till kännedomen om skandinaviska fjällväxternas Blomning och Befruktning. (Bihang till kgl. sv. Vet. Akad. Handl., Bd. 12, Afd. III, 6, Stockholm.)

Sernander, R., 1901: Den skandinaviska vegetationens spridningsbiologi. Upsala.

Skottsberg, C., 1900: Einige blutenbiologische Beobachtungen in arkt. Teile vom schwedisch Lappland. (Med. från Stockholms Högskola, Nr. 210, Stockholm.)

Sylvén, N., 1906: Om de svenska Dikotyledonernas första Förstärkningsstadium. (Kungl. sv. Vetensk. Akad. Handl., Bd. 40.)

Tedin, H., 1892: Bidrag till kännedomen om primare barken hos vedartede dikotyler. Lund.

[1] The structure and Biology of the Arctic Flowering Plants, I, Meddelelser om Grønland, Vol. XXXVI, 1908, p. 75.

Vanhöffen, 1893: Frühlingsleben in Nordgrönland. (Verhandl. der Gesellsch. für Erdkunde zu Berlin, Nr. 8 und 9.)

Warming, E, 1886: Om Bygningen og den formodede Bestøvningsmaade af nogle grønlandske Blomster. (Oversigt over d. k. danske Vid. Selsk. Forhandlinger, Kjøbenhavn.)

— 1887: Om Grønlands Vegetation. (Meddelelser om Grønland XII, Kjøbenhavn.)

A. The Morphology and Biology.

Diapensia lapponica is of decidedly cæspitose habit, a "cushion-plant" with a distinct primary root of long duration (Figs. 1 and 2). Sylvén has given a description of its early vegetative stages, from which it appears that the cotyledons, as also the other leaves, are leathery and last for two years.

The leaves are very closely set. The lateral branches are formed, as far as I can see, without any definite order. In the case of shoots terminating in flowers, vegetative shoots are formed at the base of the floral shoot and sometimes there are two opposite each other.

The evergreen leaves are stiff and leathery in consistency; and in form, somewhat oblong-elliptical and tapering towards the base; they are sessile and half encompass the stem, and are flat, but have the apex bent backward. The leaves are functional for hardly more than two years. When they die, they do not fall off, but remain for a long time on the stems in the interior of the tufts. The form of the leaf varies somewhat according to the habitat. In individuals growing in the damper and more shady localities, e. g. at Angakugsarfik on Disco (Porsild, 4650, "Shade-form submerged during spring") the leaves were somewhat longer than in the specimens growing in decidedly dry soil.

The buds have not any definite bud-scales, but they are fairly well protected, being deeply hidden among the leaves.

There is a well-marked, sparingly-branching primary root; in addition to this there are adventitious roots arising from the stem. In some cases (doubtless when growing in a sufficiently damp soil) these roots are developed abundantly and grow in towards the tufted plant, whose old leaves provide a certain amount of humus which richly provides the roots with nourishment. According to Hesselman, both ectotrophic and endotrophic mycorhiza occur very frequently in the young roots; and I am able to confirm his statement.

Fig. 1. *Diapensia lapponica* (Skådavara in Finmark).
Tuft in longitudinal section.

Sernander mentions that the *Diapensia*-tufts may break up, and the small tufts thereby formed, "may function as a means of dispersal, as they are blown about on the stony flats and thereby scatter the seeds contained in the capsules."[1] Vege-

[1] "Kunne fungera som marklöpara, idet de blasa kring på fjällhederna och derunder utportionera de i kapslerna inneslutna fröna."

tative propagation does not, however, appear to take place in this manner. From reasons unknown to me, the shoots in the tufts often die off without any special order being possibly demonstrable to exist with regard to this point; scattered among the fresh parts occur old, decaying shoots (Fig. 2).

The flowers (Fig. 3) are terminal, and, according to the investigations of Warming and Lindman they are slightly protogynous. Warming writes (1886), p. 35, "in recently expanded flowers, the corolla of which is still almost erect, the stamens are bent

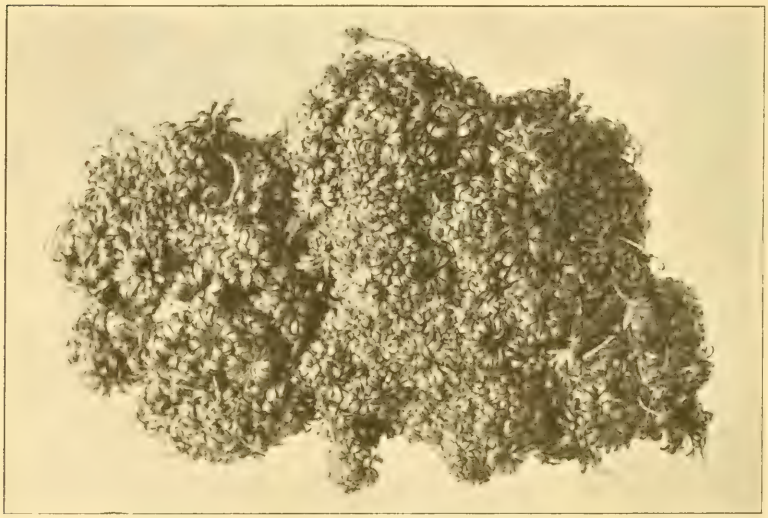

Fig. 2. Tuft of *Diapensia lapponica*
Showing how parts of the tuft have died off. (Skådavara, Finmark.)

somewhat forward, more forward than later on; but the anthers are still closed and although they open immediately after, they do not do so until they are moved somewhat away from the stigma. They always remain at the same height relative to the latter, and can touch it and shed pollen upon it, if the stamens are bent inwards in the flower, which I have often done by way of experiment. Consequently, as the open anthers are usually at some distance from the stigma, self-pollination can take

place only with difficulty, especially as the flowers are also erect. With regard to the Greenland individuals I have, however, made an observation which points to the possibility of self-pollination — I have seen that the anthers may open at an earlier date, even in the bud." As a supplement to this description given by Warming may serve the following hitherto unpublished notes by Ostenfeld, which are taken from his diary of the Ingolf-Expedition and which I have his kind

Fig. 3. (Material from Greenland).

A, A fully expanded flower seen from above; shows that the anthers are at a distance from the stigma. *B*, Corolla with stamens seen in side view, and *C*, pistil with sepal of the same flower. *D*, *E*, Pollen-grains. *F*, A young flower the corolla of which has not yet fully expanded; the anthers are open, the stigma is ripe and has already pollen upon it; the anthers being so near to the stigma, self-pollination may perhaps take place fairly easily. *G*, A young flower; the anthers are open, and the stigma is ripe; the latter has a tripartite style (see Fig. *H*). Figures and text are by E. Warming; 1886.

permission to quote: "In a bud which is in the act of opening the stamens are bent closely around the style. The latter is moist when the stamens are just in the act of opening; honey occurs abundantly in large drops at the base of the style. (Either homogamous or) slightly protogynous. The stamens are always bent somewhat inwards. No scent; the flowers were open after rain and always erect."

The structure of the flower has also been described by Skottsberg.

Hartz records that it is visited by flies.

As regards phenological observations, I may mention that Hartz found that, at Scoresby Sound, *Diapensia* opened both flowers and leaves on June 12th; and Vanhöffen in 1893 found that at Karajak (West Greenland) it opened on June 13th.[1]

According to my investigations, fertilisation and embryogeny must certainly often take place long after pollination.

The capsules may remain upon the plants far into the next vegetative period. The seeds are probably scattered very slowly. I have found a well-developed embryo in the latter.

B. The Anatomy.

W. Grevel has studied the anatomy of *Diapensiaceae* and has given what appears to be a very thorough and exhaustive description of the anatomical structure of *Diapensia lapponica*, except that of the root. For all details of a systematic-anatomical nature the reader should refer to this paper, to which I can make but few additions; my aim here is to direct attention to those features of its anatomy which are of especial value to it in relation to climate and other external factors.

The leaf. (Figs. 4 and 5). The epidermis of the upper and of the lower surface is very much thickened, especially that of the upper surface. A very thick cuticle occurs everywhere, but it is thicker on the upper surface, and is there characterized by not being of the same thickness everywhere; it sinks at times into depressions of the cellulose membrane. The whole of the external surface of the cuticle is wavy. In the outer walls the layers beneath the cuticle (in both the upper and the lower epidermis) are not quite evenly deposited; there occur, especially towards the lateral walls, canals which extend from the interior outwards towards the cuticle, without, however, reaching the latter.

[1] Cf. A. Cleve, 1901, p. 41. "Auf dem Plateau in Knospe und Blüte $^{29}/_{6}$, in voller Blüte, ausserdem mit Knospen und verblüht $^{30}/_{6}$; Kronenblätter meist weg $^{4}/_{7}$; Früchte aufgeschwollen noch nicht reif $^{6}/_{9}$."

The lateral walls are wavy, and thickened to a great extent and irregularly; in transverse section the thinner areas show up sharply against the band-like thickenings. The inner walls do not contain lignin as in *Andromeda*. Hairs are absent.

Stomata occur only on the lower surface; they are arranged more or less across the longitudinal axis of the leaf. The inner sides of the guard-cells, as well as the neighbouring

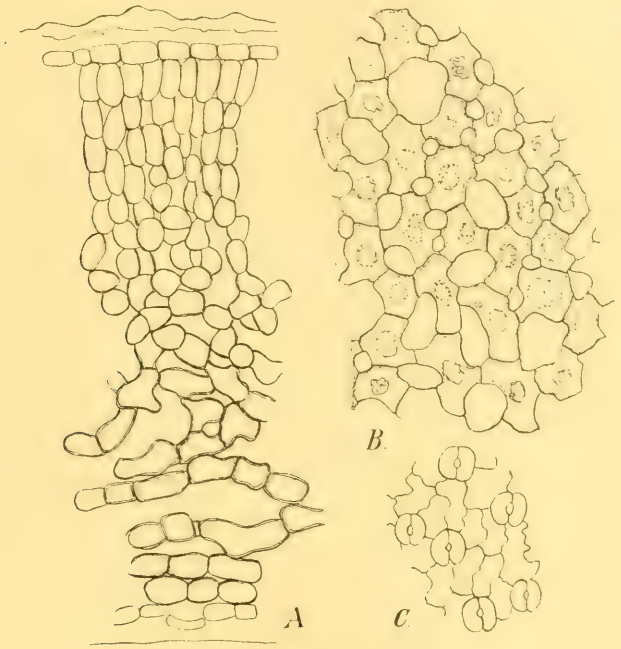

Fig. 4. *Diapensia lapponica.*
The leaf. *A*, transverse section; *B*, spongy parenchyma seen in surface view; *C*, stomata. (Greenland) (H. E. P.)

cells of the mesophyll, are covered by a thin cuticle the presence of which is demonstrated by chlor-zinc-iodine, or by Sudan III.

Chloroplastids occur in both the upper and lower epidermis (cf. Lidforss). The mesophyll consists of a well-marked palisade-tissue, formed by 2—3 layers of cells of no great height,

a palisade-like transition-zone, a spongy parenchyma with large lacunæ, and lastly, just above the epidermis of the lower surface, a zone of from one to a few layers of elongated unbranched parenchymatous cells. The cells of the spongy parenchyma are much branched — but their length is greatest in the direction of the longitudinal axis of the leaf — and they are exceedingly thick-walled. The intercellular spaces in the spongy parenchyma take up considerable room. As gradually their number and size diminish towards the palisade-tissue, the walls become less thick, until in the palisade-tissue the cells are not characterized by any special thickness of wall although always proportionably thick when compared with those of the deciduous leaves. The elongated, unbranched cells above the epidermis of the lower surface are somewhat less thick-walled than those of the spongy parenchyma, neither have they among them the large intercellular spaces which occur in the spongy parenchyma, and they doubtless form a kind of protective tissue for the spongy parenchyma. The cells of the spongy parenchyma have well-marked pores. None of the *Ericaceae* I have investigated, not even forms with highly developed intercellular spaces such as *Ledum* and *Arctostaphylos Uva-ursi*, have such thickened walls in the cells of their spongy parenchyma as has *Diapensia lapponica*.

Stereom is not developed around the vascular bundles.

In the palisade-cells of specimens from Hekla Havn (East Greenland, Nov. 1891, N. Hartz) I have observed the Kraus winter-condition of the plasma. I also found in the leaves of these specimens, and especially in their palisade-cells, an abundance of tannin; on the other hand specimens from Godthaab in the month of June did not give particularly good reaction for tannin. Oily substances, so far as they could distinctly be demonstrated to occur besides tannin (Sudan III, Osmic Acid [brown colour]), appear to be present in somewhat varying quantities at the different seasons of the year. Some summer-

specimens and the specimens from Hekla Havn gave a slight reaction for oil. As is the case in the stem, the quantity of the oil which occurs, doubtless stands in inverse ratio to the starch-contents.

The lower part of the leaf, the part enclosed by the sheath, differs anatomically from the upper part. But here I shall only

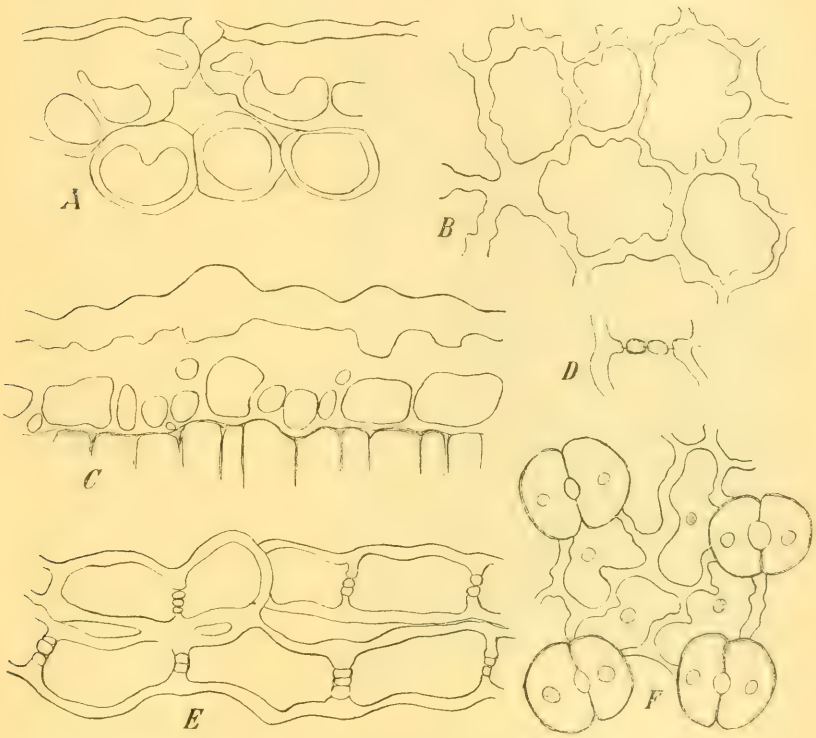

Fig. 5. *Diapensia lapponica.*
The leaf. *A*, stoma; *B*, the epidermis of the upper surface seen from above; *C*, epidermis of the upper surface with cuticle; the thickenings in the lateral walls are indicated; *D*, pores between cells of the spongy parenchyma; *E*, cells of the spongy parenchyma; *F*, stomata. (Greenland) (H. E. P.)

point out that neither stomata nor epidermis, containing water, occur in this part.

The stem (Figs. 6 and 7). The primary cortex has been figured by Tedin (Tab. I, fig. 11): it presents no features that are

especially characteristic. The structure of it is not markedly xerophytic: the inner layers are collenchymatously thickened as is the case with the sieve-tissue cork, in the secondary cortex, in the older stem.

The secondary cortex shows only a slight development of cork-tissue; the outermost layers become corky, but they cohere but imperfectly. The slight development, in the whole of the cortex of xerophytic tissue, is a natural result of the oecological form of the plant, which causes the stems not to come in direct contact with the atmosphere, and the leaves to be closely set and to fall off late - features which make all specially xerophytic tissues in the stem unnecessary.

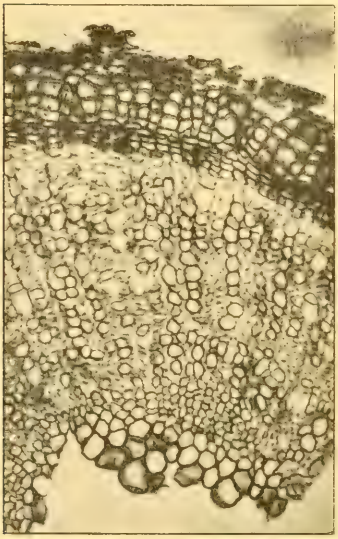

Fig. 6. *Diapensia lapponica.* Transverse section of stem: slightly mag. (Julianehaab.)

In transverse section the elements of the wood, with the exception of the vessels and some cells of the medullary rays, are peculiarly folded[1] as if the stem had experienced pressure from several directions (Fig. 7). The reason for this Grevel states is quite unknown to him, as it also is to me. It is possible that this compression is not to be seen in the living plant. In longitudinal section it can be seen that the cells do not lie exactly in the direction of the longitudinal axis of the stem, but are placed obliquely, which gives a very confused appearance to the section. Probably this is in a measure connected with the close-set leaves, the frequent formation of adventitious

[1] This shows most distinctly in preparations mounted in common glycerin, but not so well in Canada balsam preparations, such as those from which the photographs were taken.

roots, and the irregular direction of the elements of the wood.

The wood consists chiefly of vessels with bordered pits, tracheids and wood-parenchyma. Stereom (libriform cells, etc.) is not especially developed, nor are the elements which occur in the wood particularly thick-walled. There is no difference between the spring and summer (or autumn) wood, and the limits between the different annual rings are therefore not distinct. The vessels in each annual ring are usually localized in a certain zone. In a measure, this causes the annual rings to be differentiated, but as already mentioned their limits are not sharply defined.

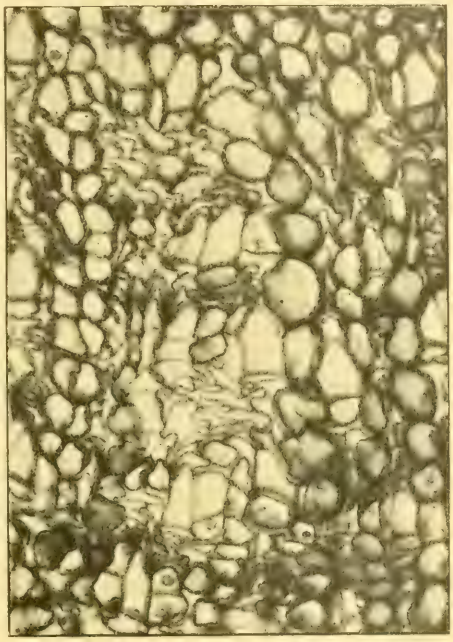

Fig. 7. *Diapensia lapponica.*
Transverse section of stem; highly mag. (Julianehaab.)

The slight development of stereom results naturally from the oecological form of the plant. Sometimes several, sometimes a few, broad primary medullary rays pass through the wood; there are only slight indications of secondary medullary rays; radial cell-rows occur, which are better defined than the other cells, but the cells have by no means distinctly the character of medullary rays.[1]

The pith consists of thick-walled cells, which form trabe-

[1] Grevel denies the occurrence of secondary medullary rays.

culae and connections between thinner-walled cells, just as in certain *Ericaceæ*, e. g. *Ledum*.

The stem contains, during winter and spring, great quantities of oil. A specimen of June 1 (Greenland: Godthaab) still contained abundance of this substance. A specimen of June 29 (Godthaab; C. H. O.) still showed indications of oil, especially in the tissue bordering on the pith. In a specimen of July 6 (Loc. ign.) oil had quite disappeared, while starch was found.

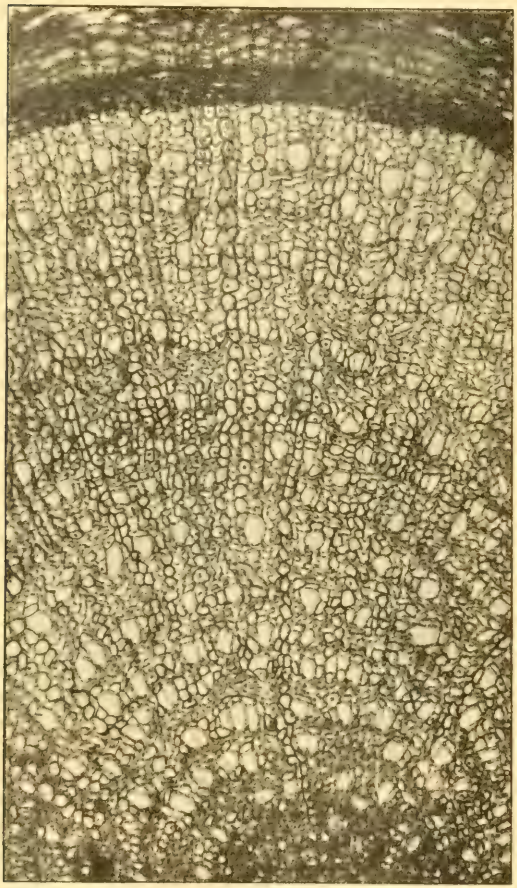

Fig. 8. *Diapensia lapponica.*
Transverse section of root; slightly mag.
(Kangersuak.)

The root. (Figs. 8 and 9). Old roots, as was also the case with the stem, are not characterized by any especial development of cork-tissue. The sieve-tissue is collenchymatously thickened as in the stem. A folding of the cells (not vessels) similar to that in the stem, was also observed. The vessels are more distinctly marked than in the stem. The formation of annual rings and medullary rays is as in the stem.

In the younger roots, as mentioned above, both ectotrophic and endotrophic mycorhiza occur (Hesselman).

C. Summary.

With regard to its flowers, *Diapensia lapponica* is entomophilous, slightly protogynous or homogamous with, however, a tendency to self-pollination.

Its oecological form is decidedly xerophytic.

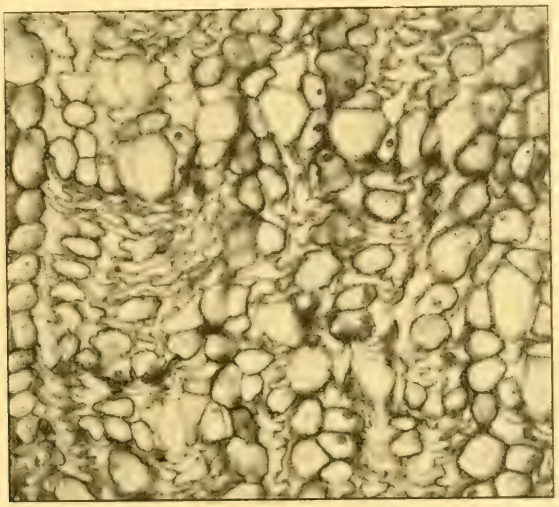

Fig. 9. *Diapensia lapponica.*
Transverse section of root; highly mag.
(Kangersuak.)

Anatomically it is only the leaves which are of xerophytic structure, as it is only these organs which come into direct contact with the atmosphere. The xerophytic structure is there indicated by the thick membranes and cuticle of the upper and lower epidermis, and by the great development of thick-walled cells in the spongy parenchyma. The structure of the leaves is not as xerophytic as that of the leaf of *Rhododendron lapponicum*, but approximates to the degree of protection presented by the latter species. Perhaps, owing to the tufted, low-growing

habit of the plant, the leaves do not require as much protection as the species just referred to. Considering both the protection indicated in the vegetative structure, and that which appears in its anatomy, *Diapensia lapponica* occupies, however, a very high position with regard to xerophytic adaptation, a position which is not surprising when we recall the fact that this species is a very old Arctic species, doubtless often a form adapted to dry soil. The palisade-tissue should rather be characterized as well-developed than as slightly developed, although the individual palisade-cells do not attain any especially great height.

7.—12.—1908.

3.

Empetraceae.

Empetrum nigrum L.

By

A. Mentz.

1909.

The greater part of the material upon which the following description has been based was brought home by different collectors from West and East Greenland, but some of it came from Iceland, the Færöes and Finmark: it is the property of the Botanical Museum in Copenhagen.

On the basis of this material, I have tried to show the peculiarities which characterize *Empetrum nigrum* in Arctic regions. As this is best done by comparison with the features this plant presents when growing in a cold temperate climate, e. g. in Denmark, I have, during these investigations, utilized also the material which I had previously collected in Danish localities.

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The primary root-system consists of a comparatively strong primary root, sometimes striking deep and branching less abundantly, sometimes striking less deep and freely putting out horizontally-growing roots. Afterwards short, abundantly-branching, adventitious roots proceed from the creeping shoot-systems, but these roots are comparatively few in number.

Root-hairs are absent. Mycorhizas appear to be rare. Only in a few instances, e. g. in material from Iceland, did I find mycorhizas—short, club-shaped, and with numerous mycelium-threads projecting from the surface.

In the first period of growth the primary shoot attains only a slight length and remains unbranched; in seedlings collected by C. H. Ostenfeld at Øfjord in Iceland, on July 30, 1886, the epicotyl measured about 7 mm., while the hypocotyl and primary root together measured about 2·5 cm. It is probable that the primary shoot does not branch until the second or third year.

The lateral shoots of the young plant are transversely

geotropic in somewhat varying degrees; they lie indifferently upon the surface of the ground; and thus arises the mode of growth characteristic of *Empetrum*. Wherever circumstances are favourable, its long, creeping shoot-systems will spread out on all sides; the growth becomes decidedly espalier-like.[1] But unfavourable circumstances of locality, caused by the substratum or by competing plant-growth; or disadvantageous circumstances of light and wind; or possibly yet other factors, very often interfere with the regular development of the espalier-like growth.

Besides the long, creeping shoots, short, erect ones also occur; sometimes on the more central portions of the single individuals, where upward growth of the new shoots is compulsory on account of circumstances pertaining to locality; sometimes where, in many habitats, the external conditions are such that the formation of short and erect shoots is in excess of that of the long and creeping shoots.

We may reasonably assume that the yearly addition to the growth of the shoots is much less in an Arctic climate than in southern regions. Naturally, in all places, it is the creeping shoots which elongate the most; their internodes are longer and their leaf-whorls more numerous than are those of the short, erect shoots. But while the length-increment on Danish heaths often amounts to about 10 cm., and sometimes even 14 or 15 cm., in Arctic regions the length of the long shoots is but 3—4 cm. at most, and often only 1—2 cm. Only in a single specimen (from Disko) did I find the increase to have been either 5 or 7 cm. These few cases, in which the length-increment was greater, are doubtless due to special conditions of the habitat—especially damp and shady soil—and also favourable conditions regarding shelter. Unfortunately it is only rarely that travellers give any information regarding this point; but N. Hartz (in the Arctic Herbarium of the Botanical Garden)

[1] Warming's term for prostrate, outspread growth.

has given a few notes regarding some individuals from East Greenland, and writes: "very long year's-shoots; damp and shady soil." In that place the greatest length-increment proved to be 4 cm., with an average of about 2 cm.

The yearly growth-increment of the short, erect shoot-systems is naturally always much less than that of the prostrate shoots, both in the regions of the far North and in cold temperate zones; and the difference of growth in the two regions is much slighter than is that of the long shoots. In Arctic regions the growth is less than one cm. Haglund (6,[1] p. 31), — who does not distinguish between the two kinds of vegetative shoots, but states that the vegetative shoots are "long shoots," — mentions that the growth of the year's-shoots on the heath at Vassijaure averaged one cm. in 1903, and that in the lowlands it was often 5—10 cm. This statement is, however, worthless, as the two kinds of shoots are not distinguished from each other. Kihlman (10, p. 226) reports the length of the year's-shoots to be generally 1—2 cm., rarely 3 cm.

When the connection between a branch-system and its mother-axis is severed, a kind of vegetative propagation may take place, but, as far as can be gathered from the literature which deals with the subject this mode of reproduction does not appear to be of great importance in the Arctic regions. Haglund alone mentions that on stony flats at Vassijaure it plays an important part, as the fruit often does not ripen there.

While the year's-shoot is quite young the epidermis is covered with numerous glandular hairs, which afterwards, and indeed fairly soon, fall off. Meanwhile, the outer walls of the epidermis thicken to a varying extent, and on the fully grown shoot, where these walls are very thick, more than one-half of them is formed by a cuticularized layer which also extends

[1] The numerals refer throughout to the papers named in the list of literature.

into the lateral walls. Beneath the epidermis a hypoderm of 1—2 layers of cells occurs, the walls of which are somewhat thickened; the inner-walls may also be cuticularized.

The primary bark consists principally of large, transparent cells, which are very thin-walled and devoid of chlorophyll, but contain numerous crystals. The bark, on the whole, has no important assimilatory tissue; its function is rather to retain water. The bark is limited internally by a distinct endodermis.

Even during the first year, in the lowermost part of the shoot, cork-formation may begin from the pericycle. With age, the thin-walled bark-tissue curls up and is shed together with the hypoderm and the epidermis. The formation of the cork has been described by Segerstedt (14, p. 64).

In the wood, the limits of the different annual rings can be distinctly seen. The vessels are very narrow, even narrower than those of the first year. The major portion of the wood consists of tracheids (see O. G. Petersen, Vedanatomi, p. 47). In relation to their age, the stems attain only a slight thickness in the Arctic regions; the width of the annual rings is naturally inconsiderable. Kihlman (10, p. 226) has examined some stems which were, on an average, 7—8 mm. in diameter, a few even 10—12 mm., the average width of the annual rings at the point of their maximum growth-radius was 0·09 mm. Schroeter (13, p. 178) cites some other measurements. Two instances from Greenland should be mentioned here. A stem from East Greenland, gathered by N. Hartz in 1900 (Liverpool coast, about 71° N. lat.), had a maximum radius of 4 mm., of which about half, the inner half, was darker coloured. The stem was about 55 years old, and the average width of the annual rings was 0·08 mm. From Ilona in South Greenland Mrs. Lundholm has sent stems of which the largest, a strongly twisted stem, had a maximum radius of about 8 mm.; the average width of the annual rings was 0·18 mm. The age of this stem was 35 years and more; but it cannot be given exactly, as the innermost

and lower parts were on the verge of decay. The cork-layer on these old stems is always thin and smooth.

The peculiar, ericoid leaves of *Empetrum* occur sometimes very closely together, as on the short, erect shoots, and sometimes at a distance (as much as 0·5 cm.) from each other, as on the longer, creeping shoots.

The leaves are functional for about three years, but may persist for a longer time in a decaying and shrivelled-up condition. When the *Empetrum*-tufts or mats, even at a great age, present an abundance of leaves, this is due to the excessive and dense branching which always occurs under favourable conditions as regards shelter, etc. But in habitats where it is exposed to the influence of a constant and strong wind it assumes a very different appearance. Kolderup Rosenvinge (11, p. 188) describes such wind-affected individuals from bleak heaths in South Greenland. He writes that old plants present "a green border which surrounds an inner part consisting only of the old, crooked branches." "The green borders are not developed all round, but only one side, in the form of a somewhat irregular, almost semi-circular curve." All the curves turn away from the direction of the prevailing wind. See photograph from the Kitsigsut-islands (p. 189, Fig. 9). Afterwards Rosenvinge describes and figures such wind-affected tufts of *Empetrum* (see p. 255 and Fig. 11) the leaves of which are very considerably reduced in number, and in which the formation of adventitious shoots is undoubtedly impossible on account of the influence of the wind.

The leaves on the shoot of the current year are obliquely erect; on the shoot of the preceding year they are more spreading and stand out somewhat at right-angles, and on still older shoots they are usually twisted somewhat backwards. They are orientated by the torsions of the extremely short stalks so that they turn their surfaces upwards towards the light.

Haglund (6, p. 31) mentions, that the leaves are consider-

ably smaller on the stony flats at Vassijaure than in the lowlands, often only half as large, but comparatively broader. A somewhat similar effect may be observed in other Arctic regions, but it should be remembered that the development of the leaves is, to a very great extent, dependent upon the nature of the habitat, and that small, poorly developed leaves can as well occur on Danish heaths as on those in Arctic regions; or vice-versa, the leaves may be as well developed on Disko, for example, as in Denmark.

Towards the apex of the shoots the leaves are very close-set. There is no other protection for the young leaf-rudiments than this dense crowding of the leaves.[1]

As is well-known, the leaves expand long after the flowering of the plant; in Denmark, in April or early in May, but in the Arctic regions naturally much later still; thus as regards Greenland the leaves do not expand until some time in July (this statement is based on the material to hand; I have in vain searched in the literature upon the subject for information regarding the leaf-expansion). As a result, the shoots have only a very short time in which to grow, for during September, without doubt, all growth is stopped. It will easily be understood that, as mentioned above, the growth-increment can on the whole be but small.

In connection with the fact that the leaves are evergreen, is their xerophytic nature; their peculiar structure is described by several authors, as Gibelli, Gruber, Warming, Börgesen (3), Wagner (18), etc. The notes by Warming (20) and Börgesen (3) on this subject are particularly interesting, because their investigations were carried out upon Arctic material; otherwise,

[1] Engler (Die natürl. Planzenfam. III, 5, p. 127) says: — "Knospenschuppen lang bewimpert." But we cannot be justified in talking of budscales proper, although it is true that the leaves, when quite young, are furnished with long hairs, which are matted together very densely in the space above the shoot-apex; this may easily be ascertained by a median section through the apex of the shoot.

I do not find any essential differences in the structure of leaves from Arctic and from non-Arctic regions (Fig. 1).

As regards the upper surface and the flanks, the outer walls of the epidermis are thick and strongly cuticularized; and the cuticle is striped longitudinally; the lateral walls are wavy. The inner walls are characterized by a thick mucilaginous layer which is noticeable along the whole of the upper surface of the leaf and round the flanks, but ceases at the entrance to the well-known "cavity" of the underside, formed by the edges of the leaf closely approaching each other, being

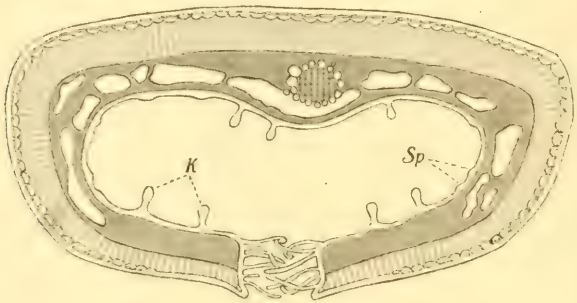

Fig. 1. *Empetrum nigrum.*
Transverse section of a leaf; magnified. The parallel lines indicate the palisade-tissue, and the tinted part the spongy parenchyma with its lacunæ, indicated by white. K, Glandular hairs. Sp, Stomata. Disko. (A. M.)

separated only by a narrow groove. This groove is closed with long hairs, densely matted together, whereby is formed, as has often been mentioned, "a calm space, free from wind." Only in the cavity, which has thin outer-walls to its epidermal cells, do stomata occur; their number is great; they lie transversely to the length of the leaf and protrude slightly. Large glandular hairs occur in the cavity.

The chlorophyll-tissue consists of 2—4 layers of very short palisade-cells and a rather lacunose spongy parenchyma. It is transversed by a large median vein and several lateral veins.

As is well-known, the flowers of *Empetrum* are exceedingly

insignificant. They occur on small drawf-shoots in the axils of the leaves, usually singly, but sometimes 2—3 together. Only when a large number occur, clustered near the apex of the vegetative shoots (they are found both upon the creeping and the erect shoots), are they conspicuous, especially on account of their purple anthers.

While in North and Central Europe it is a fact that bisexual flowers are met with only quite by chance, and also that the staminate flowers appear to be more numerous than the pistillate, yet, judging from the material to hand and the information contained in the literature dealing with the subject,[1] it must be assumed that the flowers in Arctic regions are more frequently hermaphrodite than unisexual.

As might be expected, flowering commences considerably later in the Arctic regions than in the cold temperate zones. While, in Denmark, it takes place during March or April, — the time differing somewhat according to the weather, and especially according to the amount of exposure, — we find it occurs later, the further northwards we proceed. In the Færöes, flowering is from April to the middle of May; in Iceland, at the end of May or the beginning of June; and in Greenland, at earliest and in the southern part, at the end of May, although no doubt usually during June; for, as might be expected, the time of flowering varies in the different districts of so large an area. There are some notes in the literature dealing with the subject, upon the time of flowering, especially in Greenland; and the above observations are based upon these notes as well as upon the material to hand, viz. spirit-collections and herbarium specimens. There are notes from other Arctic regions on the times of flowering which illustrate this retardation, although otherwise they differ fairly widely as regards the time;

[1] See especially Skottsberg (16, p. 12). In addition to the authors given by Skottsberg, may further be mentioned the following: — Abromeit (1), Andersson and Hesselman (2), Dusén (5).

for instance from Spitzbergen, late in July (19th and 23rd; Andersson and Hesselman). On the whole, the nature of the habitat plays an exceedingly prominent part with regard to the late or early flowering in any particular district; but with respect to phenological statements which have not been carefully illustrated and verified we cannot be too cautious; see Kihlman's remarks (10, pp. 54 and 55).

The flowers are protandrous.

Pollination undoubtedly takes place almost exclusively by the aid of the wind. E. Warming (19, p. 116) was the first to give the reasons for this, and later Skottsberg has defined them more precisely; the reasons are: — the long filaments (according to my measurements normally 7—9 mm.), which are exceedingly thin (about 0·25 mm.), and have comparatively large anthers; the perfectly smooth pollen; the large, somewhat sticky stigmas, and several other features. Skottsberg protests, with good reason, against Lindman's supposition (12, p. 35) that the flowers are sometimes entomophilous.

The formation of the flowers for the next period of growth takes place very early; in material collected Sept. 5th (Kong Oskarsham) the flower-rudiments were one millemetre long, the length of the flower-rudiments in the spring in Arctic regions.

Fruit seems to be borne abundantly by *Empetrum* in many Arctic regions, but it must develop more quickly than in the southern zones, if it is to become ripe.

Warming found young fruits "even in the beginning of July" (about 2 months later than in Denmark). He writes later: "In the beginning of August 1884 the fruit was almost ripe at Holstensborg" (21, p. 38). There is doubtless good reason to believe, that when circumstances are favourable for the development of the fruit, it ripens in August, attaining the same size as in Denmark (about 7 mm. in length and 8 mm. in breadth), and producing the same number of seeds capable of germination.

The further one proceeds northwards in the Arctic regions, he more imperfect is the development of the fruit, as might be expected; Warming (20, p. 52) cites Vahl, according to whom the fruit of *Empetrum* sometimes does not ripen in the district of Upernivik. Also other notes on the rudimentary development of the fruits are to be found in the literature dealing with the subject. In connection with this may be mentioned the very important information given by Andersson and Hesselman (2, p. 31) when they write that the fruit of *Empetrum* was never observed in Spitzbergen and that, presumably, it is sterile (?) there. Haglund (6, p. 31) says that on the stony flats at Vassijaure the fruit often does not ripen. Now, the variety (var. *purpureum* (Rafin.) DC.) described by Rafinesque, is it not just such a form, with imperfectly developed fruit? In addition to which it has been found only in Labrador, New Foundland, and in N. W. Greenland (see Simmons 15, pp. 42—43).

The fruit of *Empetrum* often persists through the winter and sometimes preserves an entire skin, and is juicy, etc.; it belongs to the "vinterståndare."[1] There is no doubt that the fruits are largely dispersed by the help of animals; both mammals (foxes, lemmings, and doubtless bears) and birds eat them in great quantities. Selim Berger (Svensk botanisk Tidskrift, 1907) mentions that ptarmigans and black grouse especially play a prominent part in transporting the seeds of *Empetrum*. The old and, in itself, reasonable conjecture of Buchenau that the seeds, in order to be able to germinate properly, must pass through an alimentary canal (B. says that of a bird), has not yet been verified by experiment.

[1] Sernander's term for plants, upon which the fruits remain throughout the winter (Den skandinav. vegetationens spridningsbiologi, p. 353).

4.

Saxifragaceæ.

1. Morphology and Biology.

By

Eug. Warming.

June 1909.

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— *hieraciifolia* 194
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Saxifraga aizoides L.

Warming, 1886 a, p. 26. Lindman, 1887, p. 61. Ekstam, 1894 b, p. 426; 1897, p. 129; 1898, p. 15. Jungner, p. 237. Abromeit, p. 37. G. Andersson och Hesselman, p. 28. Dusén p. 34. A. Cleve, p. 48. Lindmark, p. 27, pl. I, figs. 22—23; pl. II, figs. 1—3. Günthart, p. 75, pl. II, fig. I. Sylvén, p. 230.

Material in alcohol from South Greenland (Kornerup, A. Berlin, Mrs. Lundholm); from Norway: Tromsø, Finmark (Warming); Sweden; Siberia (Kjellman); Nova Zembla and Spitzbergen (Nathorst).

A creeping herb, the primary root of which dies in the course of a few years. By means of the creeping stems, which are furnished with many slender, adventitious roots, it may spread rather thickly over fairly large areas, by preference over those which are watered by a stream, or by melted snow. Many lateral shoots may be developed from a single stem, and there is no regularity as regards the situation and strength of the lateral shoots. Vegetative propagation takes place abundantly by the lateral shoots becoming independent, the connecting stems gradually dying away at the hinder end.

The lateral shoots put forth foliage-leaves from the first; scale-leaves proper are absent. The year's-shoots are not distinctly differentiated. The youngest leaves remain green during winter. The fresh leaves pass gradually into decayed ones which persist a long time.

As regards the germination see Lindmark and Sylvén. The primordial leaves are close-set, somewhat like a rosette. The plant may flower in its third year. It flowers late in summer.

The flowers appear to be quite similar to those from the Alps. The size is the same (10—13 mm.), perhaps they are somewhat smaller in Spitzbergen (Fig. 1 *E*, *F*).

The colour varies considerably. Among the specimens from Tromsö in Norway, some had pale green sepals, pale yellow petals with orange-coloured spots, and a pale green pistil; some, dull-purple-coloured sepals, dark-orange-coloured petals without spots, and a yellowish-red pistil with dark-red disk; and many intermediate forms were found between these. Lindman has made similar observations.

The petals have one vein with two lateral branches (Fig. 1 A). Scent is absent.

Protandry. The flowers are distinctly protandrous, not only those from the Alps, but also those I examined from Greenland, Norway, Sweden, Spitzbergen, and Siberia. At first the stamens are almost horizontally spread out, but afterwards they bend inwards in succession, first the antisepalous and then the antipetalous (Fig. 1 *A*, *C*). All the stamens again are widely outspread, and have been more or less emptied of their pollen, when the styles spread out and the stigmas ripen. There is, however, a short time when the stigmas and the anthers are functional simultaneously. In specimens from Spitzbergen it appeared as if the time of the development of the stigmas and the stamens did not differ very greatly, but no definite conclusion could be arrived at on the basis of the material at hand.

The nectary in all the specimens consists of a massive, ring-shaped swelling around the base of the styles, on the finely pitted surface of which numerous drops of honey may be seen to occur (Fig. 1 A, C, E, F).

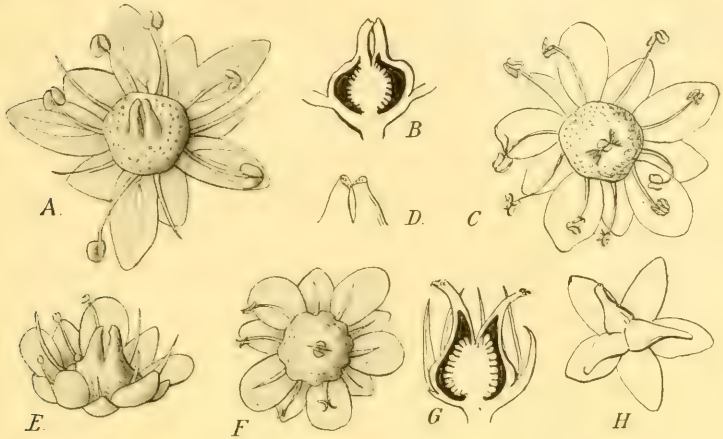

Fig. 1. *Saxifraga aizoides.*

A, Flower from the north of Norway; distinctly protandrous. *B*, Pistil of the same. *C*, Flower from South Greenland (Ivigtut); all the anthers are open, the stigmas are still unripe. *D*, Styles of the protandrous stage. *E*, *F*, Small-flowered form (Spitzbergen; Aug. 1, 1882; A. G. Nathorst); there are still four stamens with open anthers; the other anthers have been lost. *G* (from the same locality), Pistil of a flower which has quite finished flowering, and all the anthers of which have fallen off. *H*, Trimerous pistil, from the north of Norway. (E. W.)

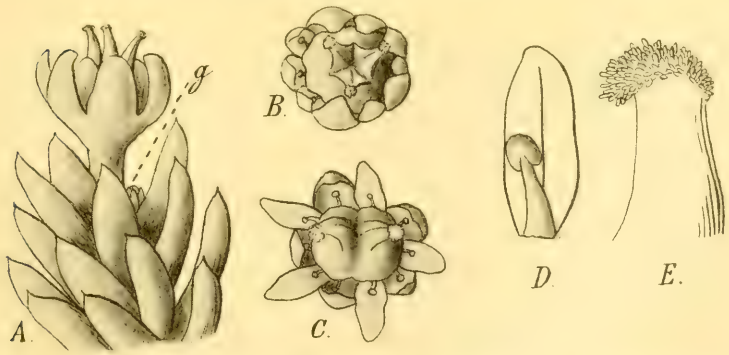

Fig. 2. *Saxifraga aizoides.*

From pistillate plants (Spitzbergen; July 27, 1882; A. G. Nathorst). *A*, Apex of a flowering shoot with trimerous pistil; *g*, a lateral shoot. *B*, Flower of same seen from above. *C*, Another flower. *D*, Petal and barren stamen. *E*, Style; there was no pollen upon the stigma. (E. W.)

Trimerous pistils often occur, especially in the terminal flowers (Fig. 1 *H*; Fig. 2 *A*, *B*). The latter are often developed much earlier than are the other flowers.

Pistillate flowers. A peculiar form has been gathered by Nathorst in Spitzbergen; its flowers are very small and have erect sepals, and small erect petals, which are about the length of the sepals (Fig. 2). The stamens are very small, smaller than the petals, and appear to be sterile (Fig. 2 *D*). As the pistils seem to be normal and have functional stigmas (Fig. 2 *E*), the flowers must be regarded as pistillate. One had a trimerous pistil (Fig. 2 *A*, *B*).

Insect-pollination appears to be the rule. Lindman observed the following insects visit the flowers in Norway (Dovre): flies, *Scæva* sp., *Bombus alpinus, B. nivalis, Vespa saxonica, Teuthredo olivacea,* and *Anaspis.* Ekstam in Sweden (Jemtland) noted the visits of flies and ants; and in Nova Zembla, of several small flies.

The fruit ripens in West Greenland, South Greenland, East Greenland (Franz Joseph's Fjord), and in Norway (Dovre), but it is not known whether it ripens in Spitzbergen and in Nova Zembla.

Saxifraga Aizoon L.

Warming, 1886, p. 27. Abromeit, p. 37. Lindmark, p. 53, pl. II, fig. 22; pl. III, figs. 5—7.

Material in alcohol from West Greenland.

The well-known rosette-shoots with short internodes in Greenland seem usually somewhat spherical, like a bulb (Fig. 3). The foliage-leaves remain fresh, either green or reddish, during winter. After dying, they persist for a long time upon the stem in a black and decaying condition (Fig. 3). Their marginal glands, which secrete carbonate of lime, are well-known (Fig. 4). The shoots obtain nourishment from adventitious roots and may live several years before they flower. After flowering, all the leaves

of the shoot die; but vegetative propagation takes place by means of the lateral shoots; the lower part of the stem of the parent shoot, which bears them, appears to be able to keep alive for a long time.

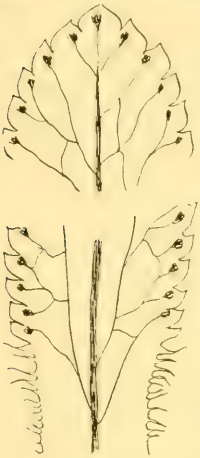

Fig. 4. *Saxifraga Aizoon.* Portions of a foliage-leaf (mag.). (E. W.)

The lateral shoots do not arise in any fixed order in the leaf-axils, and are observed most distinctly in the axils of the lower, already dead, leaves of the rosette. They often occur gathered closely together around the parent shoot, but may also be removed to a distance from the latter by a slender stem which runs along the ground and may be as much as 2—4 cm. long.

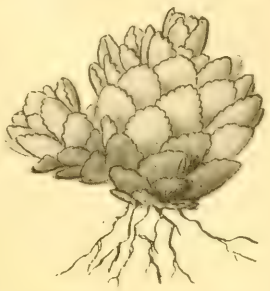

Fig. 3. *Saxifraga Aizoon.* A small plant from West Greenland (July 17, 1884); almost natural size. An inflorescence is developed upon the primary shoot. (E. W.)

In Greenland this plant appears to belong to the very late-flowering species (July).

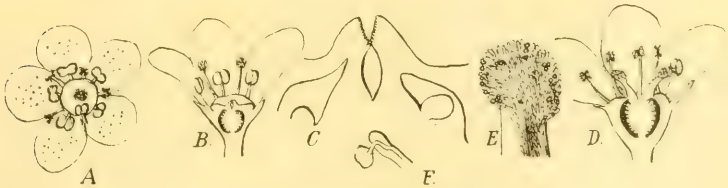

Fig. 5. *Saxifraga Aizoon.* Parts of flowers from West Greenland. *A*, A young flower, 9 mm. in diameter. The antipetalous petals are not yet functional. *B*, The same flower. *C*, Pistil of same. *D*, An older flower; the styles are spreading; the stigmas are ripe and have germinating pollen (*E*, *F*) upon them. (E. W.)

The flower appears to agree with those from the Alps. In its first stage it is 6—7 mm. in diameter; subsequently it increases to as much as about one cm. The petals are white with

many small purple dots. Around the base of the styles there is a yellow, glistening disk which secretes honey abundantly.

Marked protandry. The terminal flower is the first to expand, and is often far in advance of the others, all of which are at about the same stage of development. First the antisepalous stamens bend over the middle of the flower, then they bend back and make room for the antipetalous stamens (Fig. 5 *A*). Rarely more than 1 or 2 stamens are seen functional at the same time over the middle of the flower (Fig. 5 *A*).

The styles are at first very small and turned decidedly inwards, with the plane-surfaces of the stigmas facing each other (Fig. 5 *B*, *C*); when at the height of their development, they are out-spread, and the stigmas are set with short, almost club-shaped hairs (Fig. 5 *D*, *E*).

Self-pollination may now take place, by the stigmas reaching over towards, and touching, the anthers, in which there may still be some pollen left (Fig. 5 *D*). In this feature, the arctic flowers appear to differ from those from the Alps, self-pollination, as regards the latter, being according to H. Müller, impossible or almost so.

Fruit ripens in West Greenland (Godhavn, and other places).

Saxifraga cernua L.

J. Lange, Conspectus, pp. 61, 256. Th. Holm, pp. 46, 50. Warming, 1886, p. 3, figs. 18—20. Lindman p. 61, pl. III, fig. 28. L. Kolderup Rosenvinge, p. 678. N. Hartz, 1894, p. 36; 1895, p. 288. Ekstam, 1897, p. 133; 1898, p. 15. Abromeit, p. 34. G. Andersson och Hesselman, p. 28, figs. 13, 14. A. Cleve, p. 49. Dusén, p. 32. Lindmark, p. 74, pl. V, figs. 7—17. Simmons, p. 75. Sylvén, p. 233. Knuth, p. 452.

The plant has a short, vertical rhizome which bears both scale-leaves and long-stalked foliage-leaves (Fig. 6 *A*, *E*). The primary root most probably dies early (Th. Holm). Many bulbils may be seen to occur in the axils of the leaves on the rhizome, both of the scale-leaves and the foliage-leaves, and

also of the upper foliage-leaves, and of the bracteoles of the inflorescence (Fig. *C*). Often bulbils are produced so abundantly that the terminal flower on the main axis may be the only one

Fig. 6. *Saxifraga cernua.*

A, Basal part of a plant, about nat. size. Decayed remains of leaves on the rhizome among the fresh bulbs (northernmost Norway; Aug., 1883). *B*, A scale-leaf from the rhizome, mag. *C*, A branch of an inflorescence, about $^2/_1$; in the axils of its two uppermost bracteoles are bulbils (Norway: Finmark; July 7, 1885; E. W.). *D*, In the axil of a bract (*a*) are numerous small bulbils which belong to several generations; in the axil of *m* is a bulbil the first leaf of which is marked *α*; *1* and *2*, its first two larger scale-leaves (West Greenland). *E*, Rhizome from East Greenland (Scoresby Sound; Aug. 31, 1891; N. Hartz); *a* dead and *b* living scale-leaves. *F*, A bulbil from the axil of one of the leaves on the rhizome. (E. W.)

which is fully developed (Fig. *C*). Sometimes, however, besides the terminal flower, normal flowers are also found to occur on one or two of the uppermost lateral branches of the inflorescence (Fig. 9 *A*).

Rhizomes may be found which have internodes elongated to an unusual extent, several cm. in length (they have probably grown between moss or in shifting sand), and these afford an example of the fact that scale-leaves may both precede and

Fig. 7. *Saxifraga cernua.*
A, B, Bulbils, probably from an inflorescence, germinating.
C, A bulbil from an inflorescence with its covering of glandular hairs.
D, A bulbil of an inflorescence; the hairs are omitted. *E,* The lamina of a basal leaf.
F, Scale-leaf from the bulbil of a rhizome. (E. W., 1886.)

succeed the foliage-leaves (Fig. 6 *E*). The formation of scale-leaves indicates probably that the plant has a winter-stage. Horizontally-growing, slender runners, several cm. in length, which bear scale leaves, also occur.

In the inflorescence the bulbils are dark-red; otherwise they are white, and consist of small, thick, solid scale-leaves (Figs. 6 and 7) containing starch, which are homologous with the bases of the foliage-leaves, and often have at their apex a small lamina, which, however, in most of them, is very incon-

siderable and never develops more fully (Fig. 6 *B*, *D*, *E*; Fig. 7 *F*; Fig. 8); but in others, especially in those situated upon the floral stem, the laminæ may be fairly large and well-developed, without any indications being present of the bulbils germinating (Fig. 7 *D*). Intermediate forms between true scale-leaves and true foliage-leaves occur abundantly (Fig. 8 *A*, *C*). The bulbils are small shoots which begin with two transversely placed leaves (Fig. 6 *D*, see *a*; Fig. 8 *A*, *B*; Fig. 9 *A*), then other leaves follow spirally; but in the floral part of the shoot these leaves develop new, small, starch-containing shoots so quickly, that in a leaf-axil may occur a complex of shoots of several generations (Fig. 6 *D*), whose reciprocal relation it is very difficult, if not impossible, to unravel.

The bulbils upon the inflorescence are much smaller than are those which occur upon the rhizome.

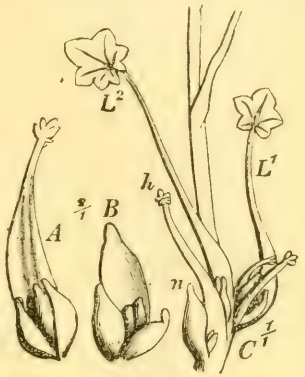

Fig. 8. *Saxifraga cernua.*
A, An imperfect foliage-leaf subtending a bulbil. *B*, A scale-leaf which is also subtending a bulbil. *C*, A portion of the basal part of a plant; *n*, a scale leaf; *h*, an imperfect foliage-leaf; both are subtending buds; L^2 does not subtend a bud. (E. W., 1886.)

That the starch-containing leaves of the bulbils serve as food for the growing shoots, may be taken for granted; those occurring lowest on the rhizome shown in Fig. 6 *E* have been emptied, while the uppermost are fresh and filled with starch; after the scale-leaves, which have been emptied, follow foliage-leaves, and after them new scale-leaves. The small bulbils on the floral shoot readily fall off and serve as organs of propagation. Lindmark, who has given an exhaustive and accurate description of the vegetative organs of *S. cernua*, has seen them and figured them germinating. The same must be assumed regarding those figured in Fig. 7 *A*, *B*.

(A "*phylloman*" form, the scale-leaves of which had deve-

loped small laminæ, was gathered by Porsild along a stream on Disko).

It can scarcely be said to be the rule for the leaves to pass the winter fully developed and in a green condition; but yet there is some possibility of this occurring — the leaves being sometimes very large and fresh during the flowering period.

The flowers are snow-white, large and fairly conspicuous. According to Lindmark 6- or 7-merous flowers are often found.

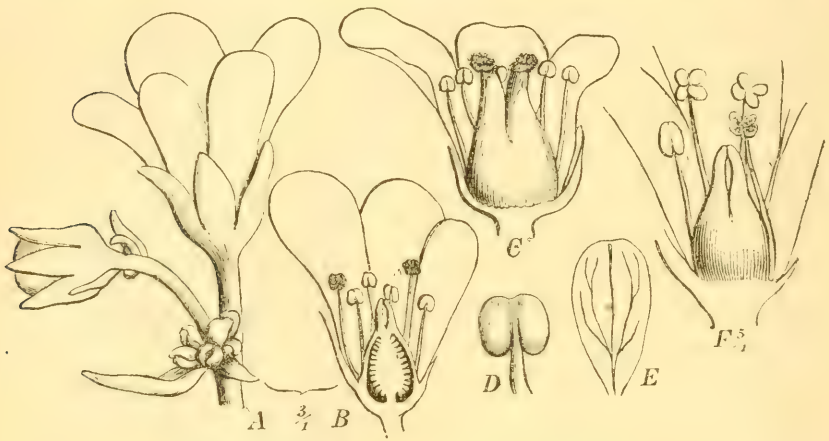

Fig. 9. *Saxifraga cernua.* (From Greenland.)
A, The upper part of an inflorescence (the hairs are omitted). *B*, Longitudinal section of the terminal flower; two antisepalous stamens have their anthers open. *C*, A protogynous flower (perhaps a transitional form to pistillate flowers). *D*, Anther. *E*, Petal; the venation may be less profuse. *F*, A decidedly protandrous flower; the anthers of the antipetalous stamens have been emptied, an open anther of a antipetalous stamen may be seen situated over the stigmas, but the latter are still unripe. (E. W., 1886.)

At first, when the petals are fairly erect, the diameter is small, 12—15 mm.; but as the petals gradually bend further out, and the corolla becomes more funnel-shaped, the diameter increases, almost to 20 mm.

The terminal flower is usually more or less irregular, as the petals of the one side are smaller than those of the other (Fig. 9 *A*, *B*, *C*). The petals may be emarginate, or rounded-off at the apex (Fig. 9 *E*).

Scent. The corolla has a faint perfume (Ekstam).

Honey is secreted at the base of the pistil. On account of the erect position of the flower, raindrops may be seen standing between the stigmas.

Protandry is the rule in specimens from Greenland, Norway and Spitzbergen, as also in cultivated specimens in the Botanic Garden of the University of Copenhagen. In the recently expanded flower the stamens stand closely against the still almost erect petals; then the antisepalous stamens bend inwards over the middle of the flower, where the styles are still short and bent towards one another (Fig. 9 *B*, *F*). Then the antipetalous stamens ripen. Almost simultaneously with the ripening of these, the styles bend outwards and the stigmas develop. Self-pollination is then possible, as the relative length of the stamens and styles is such that the stigmas may come into contact with the anthers. But nevertheless self-pollination must be difficult, and I never observed the pistils actually come into direct contact with the anthers.

Fruit does not appear to be developed; the flowers die without setting fruit. This must undoubtedly be in causal relationship to the abundant vegetative propagation. The same observations have been made by others, e. g. by Lindmark, but I am not quite sure whether we are therefore justified in regarding these flowers as staminate; this needs to be experimentally verified, and the pollen and the ovules more closely investigated.

Protogyny possibly occurs in Greenland. The stigmas in the flower shown in Fig. 9 *C* are well developed and pollen occurs upon them; some of the anthers are open, but are full of pollen, which, however, it was difficult to remove from them. Perhaps we have here a transitional form to pistillate flowers. According to Ekstam (p. 183) the flower is usually protogynous-homogamous.

Pistillate flowers occur in West Greenland, and G. Andersson and H. Hesselman also found pistillate flowers in

Spitzbergen; they were small (diam. 5—8·5 mm.), had pure-white petals, and their stamens were reduced to gland-like bodies (l. c. Fig. 13). They also found flowers, the anthers of which contained only 56 % of functional pollen. Lindmark, also, found pistillate flowers with pistils and anthers of almost equal length (l. c. p. 79).

F. cryptopetala Rosenvinge, 1892, Conspectus floræ Grönl.; Supplement II, p. 678. This form has been described as having petals half as long as the sepals, and "organa fructificationis abortiva;" it is founded upon material from Egedesminde, gathered by N. Hartz. Abromeit found, in West Greenland, forms transitional between this and the principal form. At Holstensborg I found specimens which also had very short petals, and the sepals of which were more foliaceous.

Insects visit the flowers. In Nova Zembla Ekstam saw a medium-sized fly in them.

Ripe fruit is set scarcely anywhere. Simmons writes: "the bulbillæ are probably its only organs of propagation, as the fruit was never developed so far as I have seen."

Saxifraga flagellaris Willd.

Buchenau et Focke, p. 382. Warming, 1884, p. 52; 1886, p. 25, fig. 27. Th. Holm, p. 50, pl. IX, figs. 1—7. Ekstam, 1897, p. 128; 1898, p. 13. G. Andersson och Hesselman, p. 26. Dusén, p. 34. Simmons, p. 62. Hooker, Flora Boreali-Americana, I, tab. 87. Flora Danica, tab. 2353.

Material from East Greenland (N. Hartz), Spitzbergen (A. G. Nathorst) and Siberia (Kjellman).

Rosette-plant; usually the difference between the basal part of the rosette and the rest of the shoot which terminates in the flower is greater than is shown in my Fig. 10, as the leaves in the upper part are much smaller than the rosette-leaves, much more bract-like, and occur more widely separated from each other (cf. Holm's figures).

From the leaf-axils of the rosette, thread-like runners (Fig. 10) are given off which may attain a length of 15 cm. and consist only of a single internode; they terminate in a rosette

Fig. 10. *Saxifraga flagellaris* **Willd.**
A, A flowering plant with some of its offsets (nat. size). *B*, An older isolated offset. *C*, One of the lowest leaves of an offset. *D*, Leaf from the elongated stem (twice nat. size). From Siberia; Preobraschenii Island (Kjellman, July 24, 1878). (E. W., 1884.)

which is more or less spherical because its leaves are curved upwards and inwards and are closely imbricated. The young rosettes are fixed in the soil by means of adventitious roots,

and on the decay of the runners they become separated from the parent plant (Fig. 10 *B*).

The foliage-leaves are almost obovate, and have cilia or small pointed teeth along their margin which may be more or less glandular (Fig. 10 *D*). They undoubtedly remain green through the winter. A shoot may probably remain upwards of two years in the rosette-stage before it flowers, and then the whole of it dies.

True scales-leaves are absent; and the only indications of such are the less well-developed foliage-leaves which occur basally in the rosettes (Fig. 10 *C*).

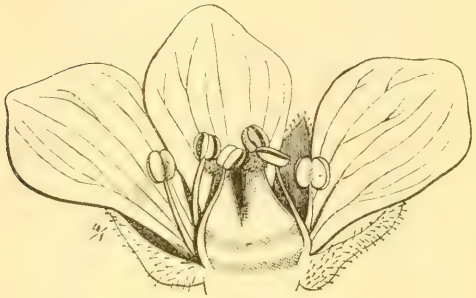

Fig. 11. *Saxifraga flagellaris.*
A flower from Spitzbergen (Tempelbay, July 17, 1882: A. G. Nathorst). (E. W., 1886.)

The corollas vary in size (the petals are from 8 to 11·5 mm. long; Andersson and Hesselman); the petals have a swelling on each side at their base. The flowers are bright yellow and scentless (Ekstam).

Judging from spirit-material, the specimens from Spitzbergen were protogynous. In the flower shown in Fig. 11 the antipetalous stamens were not yet functional, but reclined against the petals; on the other hand, the anthers of all the antisepalous stamens were open, excepting one, and were lying over the stigmas, which were fully ripe and had pollen-grains upon them. Self-pollination was in this case almost inevitable, even if the flower was protogynous at first.

Ekstam (1897, p. 128) reports that self-pollination also takes place in Nova Zembla and says: "Diese Art ist fast homogam oder schwach protandrisch." Andersson and Hesselman, like myself, found protogyny with subsequent self-pollination.

Fruit ripens in Nova Zembla (Ekstam) and in Spitzbergen (Th. Holm's Fig. 2; Anderss. and Hesselm.).

Saxifraga groenlandica L.

S. cæspitosa, Fl. Dan. *S. decipiens* Ehrh.

Lange, Conspectus, p. 62, Supplement I, p. 257. Rosenvinge p. 679.

Th. Holm, pp. 40, 51. Warming, 1886, p. 18, fig. 25. Lindman, p. 57, pl. III, fig. 25. H. Jonsson, p. 284, fig. 2. Rosenvinge, 1896, p. 107. Ekstam, 1897, p. 133; 1898, p. 18. Abromeit, p. 35. Andersson och Hesselman p. 30, fig. 15. Dusén p. 33. A. Cleve p. 49. Lindmark, p. 24, pl. 1, figs. 16—21. Günthart, p. 69. Sylvén, I, 233. Simmons, pp. 70 and 73.

This species grows in tufts, the leaves of which are numerous and close-set (Figs. 12 *A* and 14 *A*). The tufts may consist

Fig. 12. *Saxifraga groenlandica.*
A, A small tuft (natural size) from West Greenland (Disko) gathered by M. Porsild in spring (drawn by Inger Krogh). *B*, Two leaves from the same tuft. *C*, A seedling, copied from Lindmark.

of a complex of richly branched shoots, which, according to the prevailing conditions, are either crowded together so that the tuft becomes compact and pulvinate (in exposed, dry localities) or else grow loosely and have longer internodes (e. g. among damp moss). Usually each tuft obtains nourishment only from the primary root which lives a long time and becomes thick

and strong; adventitious roots may occur, but they are weak and few in number.

Vegetative propagation does not appear to take place at all, as is stated also by Lindmark and Ekstam.

The most vigorous shoots occur in the axils of the uppermost foliage-leaves and develop basipetally. But shoots may also develop lower down, even among the decaying leaves of old stems. The shoots may live several years in a vegetative condition before they flower; all the leaves on the fruit-bearing shoot die simultaneously with the setting of the fruit, but the lower parts of the stem remain alive.

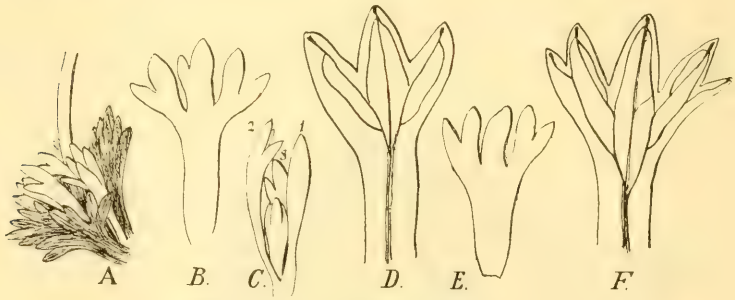

Fig.13. *Saxifraga groenlandica.*
A, A flowering shoot, between the old leaves of which the new leaves are peeping out. *B, D, E, F*, Different forms of leaves, in some the venation has been drawn. *C*, An axillary shoot; *1, 2, 3*, its first leaves. (E. W.)

The leaves are all foliage-leaves (Figs. 12, 13, 14); they persist for several years in a decayed condition, and may be found upon the stems right down to the root without the occurrence of intermediate leafless portions. The upper leaves on the shoots remain quite green throughout the winter (Fig. 12); see H. Jonsson, Fig. 2; Lindmark.

In the beginning of spring, fresh leaves and flowers are seen appearing among the older ones at the apex of the shoots (Fig. 13 *A*). The flowers are formed during the year previous to that in which they open, and they pass the winter with well-developed anthers and pistils (Fig. 15 *E*); but according to Jonsson the integuments of the ovules are not yet developed.

Andersson and Hesselman write: "When winter comes and interrupts the work in the plants, numerous flowers are found in this species."

The germination of the seed has been described and

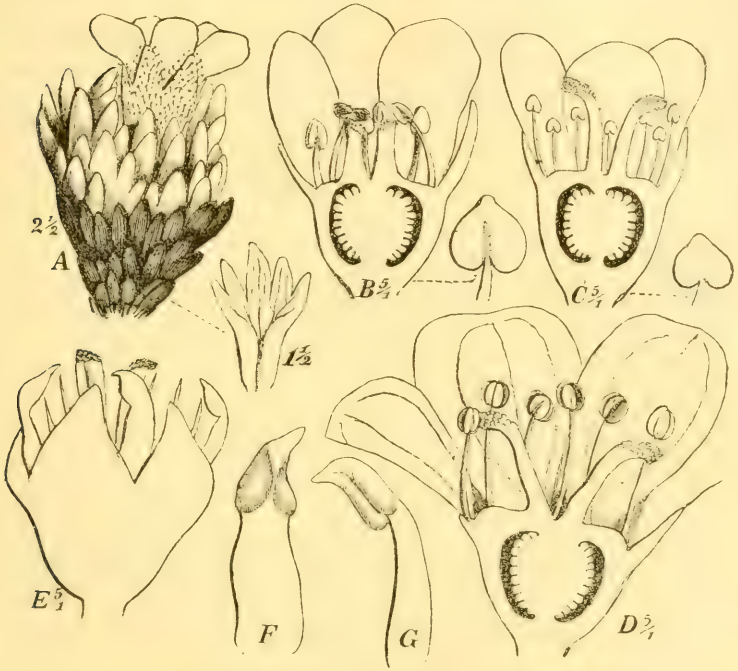

Fig. 14. *Saxifraga groenlandica.* (From Greenland.)

A, A shoot gathered early in spring (June 29, 1884) at Godthaab; the hairs are partially omitted; in the flower the stigmas and anthers were fully developed and in contact with each other; the accompanying leaf belongs to this shoot. *B*, From the same locality; four antisepalous stamens are bending over the stigmas, with their anthers open; the stigmas are not yet full-sized, but nevertheless, they are able to retain the pollen-grains. *C*, a pistillate flower from Godthaab; although young, its stigmas are well-developed; the anthers are abnormally small (compare the accompanying figure with that corresponding to it in *B*). *D*, Flower from Umanak (Eberlin, July 15, 1885); the stigmas are thrust in between, and in contact with the anthers which still contain pollen. *S. groenlandica* var. *cryptopetala* Berlin, from Holstensborg (Aug. 6, 1884). *E*, *F*, *G*, A flower, and two petals. The anthers of the normal stamens have been lost. (E. W., 1886.)

figured by Lindmark; lateral shoots are developed at an early stage in the axils of the lower primordial leaves (Fig. 12 *C*, after Lindmark).

The flowers vary greatly as regards their size (5—15 mm.)

and colour. The petals may be white, yellowish-white, greenish-yellow or reddish, and have three yellowish-green stripes (Fig. 14 *D*); they are erect or bent somewhat outwards, hence the rain-drops may collect among them. During rain the flower is wet down to its base.

Scent. According to Ekstam it has a faint, pleasant scent in Nova Zembla, but no scent has been noticed in Spitzbergen.

Honey is secreted abundantly by the yellow, glistening base of the pistil.

The flowers vary greatly as regards their development,

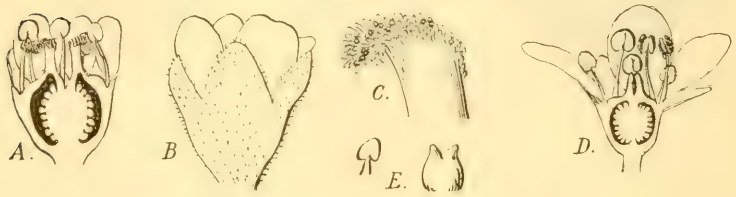

Fig. 15. *Saxifraga groenlandica.*

A, B, Small-flowered form with greenish-yellow petals, homogamous or perhaps protogynous flowers. The anther of one of the antisepalous stamens is open (Spitzbergen July 1, 1882; A. G. Nathorst). *C,* Ripe stigma; there are many pollen-grains upon the stigma (West Greenland (Godthaab); June 29, 1884). *D,* The flower is still small; it is protandrous. The antisepalous stamens are erect and some of their anthers are open. The styles are quite unripe. *E,* Stamen and pistil (about $^8/_1$) of a flower gathered Dec. 31, 1893, in East Iceland; H. Jonsson). (E. W.)

some being protandrous, some protogynous, and some homogamous.

Protandry. In Greenland I found slight protandry to be the rule. In the recently expanded flower all the stamens are erect or bent somewhat outwards and lie against the petals; but afterwards the antisepalous stamens begin to bend inwards towards the middle of the flower, so that the open anthers are placed above the still unripe stigmas. Then those stamens bend backwards and the antipetalous stamens perform the same movements, but before the stamens have finished making these movements, the styles have spread out and the stigmas have become ripe. In Fig. 14 *B* it is only the anthers of the four antisepalous stamens which are open, but even at that time the

stigmas, as yet not fully developed, are able to retain the pollen-grains; self-pollination will even at that time be able to take place.

In other cases the flowers were more highly protandrous. In cultivated specimens (Hortus Hafniensis) the terminal flower was so protandrous that self-pollination was impossible; here the corolla had attained a diameter of as much as 15—20 mm.[1] From Spitzbergen Ekstam reports "homogamy, with marked inclination to protandry."

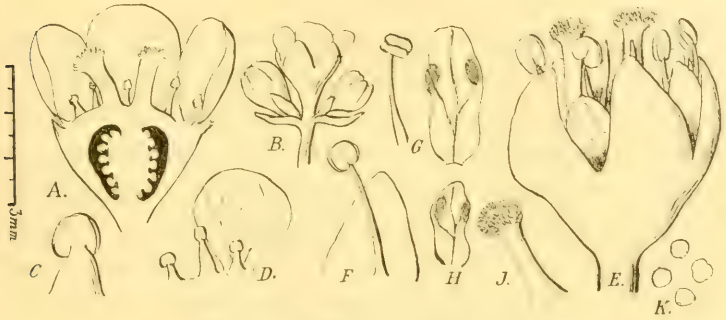

Fig. 16. *Saxifraga groenlandica.*

A—D, Pistillate flower from Iceland (Dyrefjord; June 10, 1895; C. H. Ostenfeld); *A*, flower in longitudinal section (with the accompanying scale): *B*, part of an inflorescence (3/1); *C, D*, petal and stamens of Fig. *A*.

E—K, forma *cryptopetala* from West Greenland (Egedesminde; leg. N. Hartz). *E*, A flower (about 8/1); the petals are considerably smaller than the sepals. *F*, A sepal with antisepalous stamens. *G, H*, Petals and an antipetalous stamen, *J*, Style. *K*, Pollen-grains appear to be quite normal. (E. W.)

Protogyny occurs also, at any rate in Spitzbergen (Warming, 1886). According to Andersson and Hesselman the f. *uniflora* is "always protogynous" in Spitzbergen. In Nova Zembla the flowers were "in numerous cases protogynous-homogamous" (Ekstam, 1897).

Homogamy. Lindman reports that in Norway (Dovre) the flower is homogamous; in Nova Zembla Ekstam found some flowers which were "almost homogamous." With regard to

[1] Günthart found cultivated specimens in Switzerland so highly protandrous that "between the staminate and the pistillate stage a short neutral, i. e. sexless intermediate condition occurred."

Spitzbergen he says: "The autumn-flowers differ in being more markedly homogamous." Nathorst has already reported that, in addition to the usual form, another occurs with greenish-yellow flowers, which are considerably smaller (generally only 5—6 mm. in diameter), are homogamous, and are self-pollinated; compare Fig. 15 *A*, *B*.

Insect-visitors. Ekstam found many different species of flies and other *Diptera* in the flowers in Nova Zembla and in Spitzbergen; Lindman similarly found *Formica fusca*, on the Dovre.

Self-pollination. I wrote in 1886: "In few species is self-pollination so evident as here; at a time of the year when the greater part of the country is still covered with snow, and when there is scarcely any sign of insect-life, the anthers may be found open and in immediate contact with the stigmas, with germinating pollen-grains upon the latter; even on the 2200 feet high plateau on the island of Disco, near the perpetual snow, did I observe this, and, also, the remains of ripe fruit from the previous year."

Self-pollination is mentioned by Lindmark as taking place regularly, and it is reported and figured by Lindman; Ekstam says that self-pollination occurs frequently in the protogynous-homogamous flowers in Spitzbergen, but is "prevented" in the protandrous and homogamous ones.

Pistillate flowers. I have often found the terminal flower in the inflorescence to be differently developed from the other flowers; its styles developing quickly and bending outwards, and its stigmas becoming highly papillose while the anthers are still entirely closed (Figs. 14 *C*; 16). But as these anthers are smaller than usual, are never opened, and appear to have abnormal pollen, the flower must be regarded as a pistillate flower with large staminodes. I have observed such terminal flowers in material from Greenland, Spitzbergen and Norway, as also in cultivated specimens (Hortus Hafniensis).

Ekstam found similar pistillate flowers in Nova Zembla; he writes: "During autumn, closed or half-closed flowers are often put forth, in which only the pistils are developed, while the anthers are rudimentary." Andersson and Hesselman also found pistillate flowers in Spitzbergen and in Beeren Eiland; they write: "the anthers never open," and Lindmark writes: "Truly pistillate flowers are common; it is almost the rule for the terminal flower to be more or less pistillate" (see his Fig. 21, Pl. I).

Forma *cryptopetala* Berlin (Sv. Vetensk. Akad. Öfversikt, 1884, p. 38). Berlin found in West Greenland (Egedesminde, Auleitsivikfjorden), and in East Greenland, a form with ovate-lanceolate petals of the same length as the sepals, the stamens of which are longer than the sepals. "The petals are swollen at the somewhat drawn-out apex, which suggests that they are being transformed into stamens." An exactly similar monstrous form I examined in material from West Greenland (Holstensborg, Aug. 6, 1884; see Fig. 14 *E*, *F*, *G*). On the same individual may be found quite normal flowers and «cryptopetalous" ones such as that figured, the petals of which have, towards their apex, thick, yellowish margins, indicative of anthers.

Another form showing similar instances of abnormality, but with smaller petals, was gathered by N. Hartz in West Greenland (Egedesminde); it appears to have ordinary hermaphrodite flowers with normal pollen and stigma; only the petals are being transformed into stamens (Fig. 16 *E*—*K*). In regard to this point Hartz writes: "sets ripe fruit; on two large tufts which have been examined, only cryptopetalous flowers were found. Protogyny was found. Self-pollination must easily be able to take place."

This cryptopetalous abnormality was also met with in Spitzbergen with "the petals transformed into stamens" (Andersson and Hesselman, Fig. 15); easy transitional stages between petals and stamens occurred.[1]

[1] Roper has in *Saxifraga granulata* observed a form "*apetala deca-*

Other deviations were also met with. In South Greenland Mrs. Lundholm found double flowers.

Fruit ripens abundantly in Greenland, Jan Mayen, Iceland, the Færöes, Spitzbergen, Beeren Eiland, Siberia and in Arctic Scandinavia. It ripens so regularly that fertilization must be absolutely certain, probably by means of self-pollination.

Saxifraga hieraciifolia Waldst. et Kit.

Lange, Conspectus, p. 59. Th. Holm, p. 52. Warming, 1886 b, p. 17. Ekstam, 1898, p. 132; 1897, p. 10. G. Andersson och Hesselman, p. 21. Dusén, p. 31. Lindmark, p. 49.

Knuth, p. 448.

Only alcohol-material from Spitzbergen and Siberia has been at my disposal.

A herb of the *Primula*-type; agrees altogether fairly closely with *S. nivalis*. The rhizome is erect or somewhat oblique; fairly thick and robust, and furnished with long, vigorous adventitious roots; it gradually dies away at the hinder end. It may either be branched, or set with buds.

Branching. The shoots may remain for several years in the rosette-stage before they flower. On a flowering shoot the principal lateral bud, which is situated in the axil of one of the uppermost leaves of the rosette, may be so fully developed while the parent shoot is flowering, that its foliage-leaves principally serve to form the rosette at the base of the inflorescence, the foliage-leaves of the parent shoot being for the most part dead.

The leaves are all foliage-leaves, which are often more or less red.

The flowers are small and rarely open in a stellate manner, but remain more or less closed with small, erect or slightly inwardly-bent, petals (Fig. 17). The diameter is 5—10 mm.

pentandra", the petals of which were also metamorphosed into stamens (Botan. Zeitg., 1856).

(Nova Zembla; Ekstam). The petals are shorter than the sepals or equal them in length; they are dark-red. The stamens perform the usual movements. Honey is secreted by the pistil-base which recalls that of the Umbelliferæ, each style having at its base a sinuously-angular nectary disk (Fig. 17 *B*). This is also the case in *S. nivalis* and *S. pensylvanica*. Scent is absent (Ekstam).

The flowers are reported by Ekstam to be in Nova Zembla "decidedly protandrous; even in the bud one or several of the anthers may sometimes be open;" but from Spitzbergen he reports "protogynous-homogamous; the stigmas move away

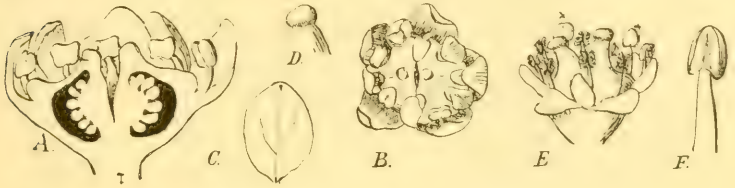

Fig. 17. *Saxifraga hieraciifolia.*
A, A young flower (5/1); its anthers have not yet opened and its stigma does not appear to be ripe. From Siberia (Chabarova; July 31, 1878; Kjellman). *B*, A similar flower, magnified as *A*; from Spitzbergen (July 1, 1882; A. G. Nathorst). As yet none of the anthers have opened. *C*, Petal. *D*, Style with stigma. *E*, A flower from Spitzbergen (July 27, 1882; A. G. Nathorst). All the anthers are open except those of the two antipetalous stamens, marked x. *F*, Stamen. (E. W.)

from each other and become glistening-papillose, even before the anthers have reached their full development." On spirit-material from Spitzbergen and Chabarova I found the flowers to be homogamous or perhaps slightly protandrous.

According to Ekstam (p. 132) self-pollination is sometimes possible by the styles bending outwards simultaneously with an inward movement of some of the stamens (Nova Zembla). In his paper he writes of Spitzbergen: "In the greater number of cases, self-pollination is probably prevented by the fact that the stigmas are situated considerably above the level of the anthers, owing to the length of the styles. Sometimes, however, they stand on the same level." The flowers figured by

me (Fig. 17) are homogamous and illustrate the latter condition. I have found the anthers to be in contact with the stigmas, but as only spirit-material is at hand and I have had no opportunity of examining living flowers, there is no certainty that this has not been occasioned by violence.

Insect-visitors. In Spitzbergen Ekstam saw a fly visit a flower. It is noteworthy that the stigmas are not highly papillose, as is the case in most of the other species, but are spherically rounded off without papillæ and covered by mucilage (Fig. *D*). In this feature this species resembles *S. nivalis*.

Several times I found trimerous pistils in terminal flowers. Lindman and Ekstam also found 3- and 5-merous pistils.

Fruit. According to Ekstam, Kjellman found ripe fruit in Arctic Siberia; and Andersson and Hesselman report that the seed ripens regularly in Spitzbergen.

Saxifraga Hirculus L.

Lange, Conspectus p. 64. Warming, 1886 b, p. 25. Ekstam, 1897, pp. 130, 180; 1898, p. 14. G. Andersson och Hesselman, p. 27; Dusén, p. 34. Lindmark, p. 32. Silén, p. 86. Simmons, p. 64.

The Arctic plants are often low and somewhat tufted. From the base of the erect flowering shoots are given off, in Danish specimens, slender runners in basipetal succession, and with a more or less subterranean course. These runners may be either short or long; they form many slender roots and their leaves are developed to a varying extent as foliage-leaves. The runners, whose course is most subterranean, are very slender and bear scale-leaves (Fig. 18). The primary root probably dies early. Vegetative propagation takes place by the lateral shoots becoming isolated when the irregularly-branched rhizomes gradually die away at the hinder end.

According to Lindmark the rhizome may have 2—3 or several year's-shoots.

The shoots may remain for a few years in a vegetative condition before they flower.

According to Lindmark the youngest foliage-leaves remain green during the winter; on the flowering shoots, either the greater part, or all of the foliage-leaves of the previous year are brown and dead. Of the rejuvenating shoots, some may come into flower soon after the parent shoot itself flowers.

The flower. I myself only examined material from Spitzbergen and Denmark. The diameter of the flower from Spitz-

Fig. 18. *Saxifraga Hirculus* L.

A, A flowering plant (almost nat. size) from Spitzbergen (July 7, 1882; A. G. Nathorst). *B*, Part of a flowering plant from Denmark (almost nat. size); *a*, dead runner; *b*. *c*, living runners. *C*, Apex of the living runner *c*. (Drawn by E. W.)

bergen is, in its staminate stage 10—15 mm., in its pistillate stage, 13·5—18 mm. (Andersson and Hesselman), and from Nova Zembla 12—25 mm. (Ekstam).

The petals are bright yellow with lemon-coloured dots, and have at their base a peculiar swelling on each side (Fig. 19 *C*). They are 2—3 times longer than the sepals.

Scent. The flower is scentless, and honey does not appear to be secreted, "unless perhaps in very small quantities at the base of the stamens or in the folds of the two protuberances at the base of the petals" (Ekstam).

Protandry. The flower is markedly protandrous, as is

also the case with the Danish specimens (Fig. 19 in which the antisepalous stamens are bent inwards, and have some of their anthers open; one stamen (marked x) has already bent backwards; the antipetalous stamens and the pistil are still unripe). All the antipetalous stamens may be bent forwards with their anthers open, before the pistil is ripe.

Pistillate flowers with small anthers devoid of pollen, and forms showing all the transitional stages between these and the usual flowers, occur in Spitzbergen (Andersson and Hesselman).

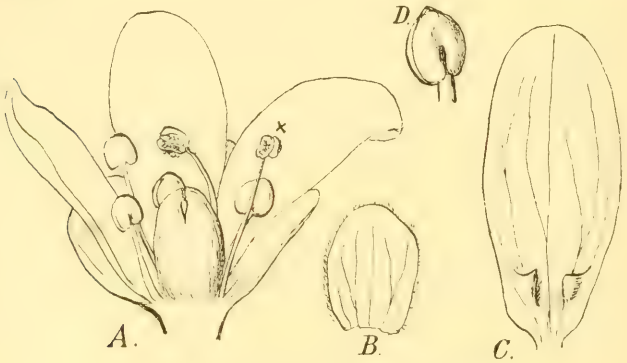

Fig. 19. *Saxifraga Hirculus* L.
Spirit-material from Spitzbergen (Recherche-Bay; July 7, 1882; A. G. Nathorst). *A*, A distinctly protandrous flower; one of the stamens is bending over the middle of the flower; the one marked x has already bent backwards. *B*, Sepal, *C*, Petal. *D*, Anther. (Drawn by E. W.)

Ripe fruit is said to be developed in Spitzbergen, but probably not every year (Andersson and Hesselman). Almost ripe fruit was found in Nova Zembla (Ekstam).

Insects-visitors. In Nova Zembla and in Siberia Ekstam and Kjellman saw different kinds of small, large, and medium sized flies and other *Diptera* visit the flowers.

Saxifraga nivalis L.

Lange, Conspectus, p. 59. Rosenvinge, 1892, p. 177. Th. Holm, 1885, p. 52. Warming, 1886 b, p. 14, fig. 24. Lindman, p. 58, tab. II; fig. 24. N. Hartz, 1894, p. 4; 1905, p. 288. Rosenvinge,

1896, p. 107. Erstam, 1897, p. 131, 1898, p. 11. Abromeit, p. 32. G. Andersson och Hesselman, p. 22. Dusén, p. 32. A. Cleve, p. 48. Lindmark, p. 45, tab. II, figs. 18—20; tab. III, fig. 1. Simmons, p. 67. Sylvén, p. 230.

Knuth, p. 452.

A herb of the *Primula*-type, tufted in habit, with an erect or else more or less oblique rhizome (Fig. 20), which is

Fig. 20. *Saxifraga nivalis.*
A, A specimen (slightly reduced) from Disko, gathered by M. Porsild; *K*, a lateral shoot. *B*, A leaf (somewhat mag.) from Iceland. *C*, A leaf of *S. nivalis*, f. *tenuis* from Jan Mayen. (E. W.; drawn by J. Krogh.)

usually short, but sometimes attains a length of as much as 5—6 cm. and is thick and strong, and may be rather densely branched. Numerous adventitious roots occur. The specimens from Cape Tcheljuskin (Siberia) formed dense tufts, the nume-

rous thick, short, erect rhizomes being united into a single mass, and bearing many adventitious roots.

All the leaves are foliage-leaves and occur in a rosette. They may live through the winter in a fresh, green condition. At Upernivik in places recently freed from snow, erect, green leaves occurred, surrounded by the dead parts. The leaves are sometimes reddish, especially on their undersides.

Lateral shoots are developed in the axils of the flowering shoots even from the commencement of their flowering-period, the principal bud being in the uppermost leaf-axil, and the others in basipetal succession. The principal bud may develop so quickly that it makes the inflorescence appear lateral, and may flower simultaneously with the parent shoot. The shoots may remain several years in a vegetative stage before flowering. Specimens with several inflorescences, produced by rapid growth of the lateral shoots of a flowering shoot, occur fairly frequently.

Seedlings are described and figured by Lindmark. In 1877 I sowed seed in April, and in August 1878 the seedlings had close-set rosette-leaves and fibrous roots, but were not yet branched.

The flowers pass the winter well-developed, and are among the first to open in spring. Specimens from the north coast of Siberia had inflorescences for the next year distinctly developed even by the end of August. The flowers are small and inconspicuous, the diameter is only 5—8 mm.; in Siberia some measured 10 mm. across (Kjellman, according to Ekstam). The calyx is often brownish-red in colour, and the petals are whitish, or greenish yellow, or reddish to light pink or white with red tips. They are erectly-spreading, and of the same length as the calyx or somewhat longer (Figs. 21, 22). The stamens have reddish or yellowish filaments and pale minium-red anthers. The styles often become dark-red in older flowers.

Honey is secreted by the glistening, greenish base of the

styles which is usually sinuate along its margin (Figs. 21, 22). After rain a large collection of water, evidently containing nectar, can be seen at the bottom of the flower. Scent is absent (Ekstam).

According to field-notes made by me, the Greenland spe-

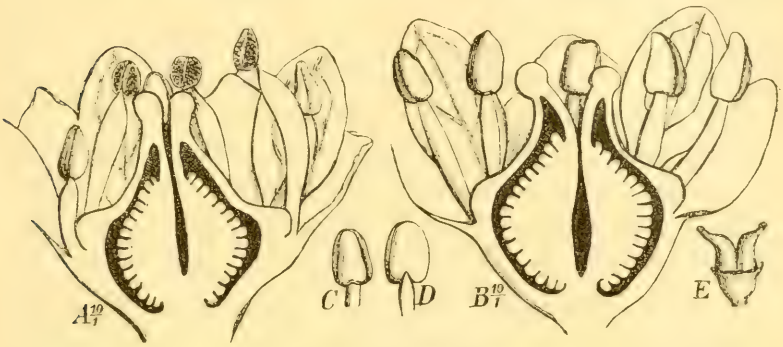

Fig. 21. *Saxifraga nivalis.*

A, A flower from West Greenland (July 6, 1884). The antisepalous stamen to the left, has its open anther just above the stigma, which has germinating pollen-grains. The anthers of the antipetalous stamens are closed. *B*, A younger flower which is protogynous (north of Norway: Tromsö; June 27, 1885); all the anthers are closed, but the stigmas are ripe. *C, D*, Anthers from the ventral and the dorsal side. *E*, Unripe fruit (West Greenland). (E. W., 1886.)

Fig. 22. *Saxifraga nivalis.*

A, Young flower of *S. nivalis* var. *tenuis* from Spitzbergen (July 11, 1882; A. G. Nathorst); the anthers are still closed; the stigmas appear to be ripe. *B*, Style and stigma from *A*. *C*, An unusually small flower (magnified as *A* and *E*); all the anthers are open; the styles are spreading so that the stigmas touch the anthers; self-pollination will take place (Norway; Aug. 20). *D*, A stigma with pollen-grains; the antipetalous stamens in this flower were still closed, the antisepalous were open, but still contained some pollen. Gathered by Kjellman in Siberia: Cape Tscheljuskin.

E—J, Flower from West Greenland (July 28, 1885; S. Hansen); some of the anthers (*H, J*) are barren; others (*F*) are open, but the pollen-grains (*G*) do not appear to be quite normal. (E. W., 1886.)

cimens do not appear to differ from those from Scandinavia, Spitzbergen and northern Asia.

Protandry has been observed in Greenland, Norway (Lindman), Sweden (Axell), and Nova Zembla (Ekstam), and I found cultivated specimens (Hortus Hafniensis) which were slightly protandrous.

Protogyny. It appears to be the rule for the flowers to be slightly protogynous (Greenland and Nova Zembla), but if so, homogamy ensues very soon. The styles bend outwards but slightly, and the stigmas, which in this species, as in *S. hieraciifolia*, are evenly rounded, glistening and without papillæ (Fig. 22 *B*), are usually able to retain pollen before any of the anthers of the still quite erect stamens are open (Fig. 21 *B*). The plant appears, however, to be homogamous during the greater part of the flowering-period, and self-pollination seems to be very common, and is, at any rate, easily possible in case cross-pollination does not take place. The movements of the stamens are those usual in the other species. But the stamens almost always stand fairly erect, or else they lean slightly forward over the middle of the flower, and even touch the stigmas with their anthers (Figs. 21 *A* and 22 *C*).

In other flowers I found the stamens somewhat spreading when they began to be functional (as in Fig. 21 *B*), so that here, self-pollination by direct contact does not seem to take place. The specimens from Norway appear to me to be less distinctly self-pollinating than are those from Spitzbergen and Greenland.

Insects, according to Ekstam flies, visit the flowers.

Fruit usually ripens in West Greenland, in Ellesmere Land (Simmons: "fruited richly"), Jan Mayen, Iceland, Norway, the Færöes and Siberia. Half-ripe fruit was found by Dusén and Bay in East Greenland, by Ekstam in Nova Zembla, and by Andersson and Hesselman in Spitzbergen.

Pistillate flowers. In some specimens gathered by

Dr. S. Hansen in West Greenland, the styles were considerably longer than the stamens, and as the anthers were also smaller than usual, but yet were open, and as the pollen-grains appeared to be abnormal and imperfect these should probably be regarded as pistillate flowers or as transitional in that direction (Fig. 22, *E—J*).

Saxifraga oppositifolia L.

Lange, Conspectus, pp. 66, 257. Rosenvinge, 1892, p. 680. Th. Holm, p. 40. Warming, 1886 a, p. 29, fig. 28; 1886 b, pp. 113, 118. Lindman, p. 56, pl. II, fig. 21. Bonnier, p. 513. N. Hartz, 1894, p. 4; 1895, pp. 242, 287. H. Jonsson, p. 283, fig. 1. Rosenvinge, 1896, p. 107. Ekstam, 1897 a, p. 127 (Nova Zembla); 1897 b, p. 12 (Spitzbergen). Vanhöffen, p. 38. Abromeit, p. 38. G. Andersson och Hesselman, p. 23, figs. 8—12. Dusén, p. 35. A. Cleve, p. 48. Lindmark, p. 19, pl. I, figs. 8—15. Sylvén, p. 229. Simmons, p. 60.

H. Müller, p. 98, fig. 31. Knuth, p. 444. C. Schröter, p. 540.

Material from West Greenland (Kornerup, Holm, Warming, Ryder, Hartz), East Greenland (Hartz, V. Eberlin, Deichmann, Knutzon), Iceland (Hj. Jensen, Helgi Jonsson, Stefansson), the Færöes (Warming, Börgesen, Helgi Jonsson), Nova Zembla (Th. Holm), Norway (Warming).

This *Saxifraga* is the one with the most extreme Arctic distribution, and it flowers earliest in spring; scarcely has the snow melted — indeed, it may not yet have done so — when the flowers, which have passed the winter in a well-developed condition (Fig. 26 *D*), expand. Even in March, open flowers may be found in West Greenland (March 26; J. Vahl).

This species is a perennial herb, which has a tendency to become a sub-shrub as the branches become woody; it varies somewhat in form, hence Andersson and Hesselman even established a forma *reptans* and a forma *pulvinata*. These are probably only modifications occasioned by circumstances pertaining to locality (cf. also Simmons).

In some plants the stems are prostrate, have more or less elongated internodes, and attain a length of from 10 to 30 cm. (Fig. 23; Fig. 24 *H—J*); many lie quite freely upon the ground, but some are attached to the soil by adventitious roots. The primary root remains alive for several years, ordinarily, no doubt during the whole life of the plant, but sometimes the adventitious roots become strong and the plant may multiply

Fig. 23. *Saxifraga oppositifolia.*
(From the East of Iceland; Dec., 31, 1893.)
A prostrate shoot with two erect floral shoots bearing the dehisced capsules of the previous year and also several younger floral shoots, the fully-developed flowers of which are enclosed between the fresh green leaves (Helgi Jonsson, 1895; drawn by C. Thornam).

by vegetative propagation. This, however, appears to occur comparatively rarely. In forma *reptans* (Andersson and Hesselman) the adventitious roots appear to be more abundant than is usual.

The prostrate shoots give off erect floral shoots the leaves of which are usually so close-set, and the internodes so short, that they become square (Fig. 24 *B*, *E*; Fig. 25 *A*). The leaves are generally opposite and decussate (Fig. 25 *A*, Fig. 24 *F*),

sometimes, however, the leaf-pairs do not cross each other exactly at right angles (Fig. 24 *G*). The stems of this form may form a low carpet of greater or lesser extent.

The form with a pulvinate habit, has usually only a primary root; it gives off lateral branches, more or less erect, forming dense, semi-globular cushions which, according to Andersson and Hesselman, may attain a diameter of 20—30 cm. and a height of 10 cm. Prostrate branches appear sometimes to be quite absent. I have gathered similar specimens, cushion-like in habit and richly-flowering, in Finmark; and in the "Riksmuseum" in Stockholm, there is a specimen in spirit (in a glass measuring 5 cm. in width) gathered by Nathorst, which, is as large as a clenched fist, and has about 120 flowers.

Fig. 24. *Saxifraga oppositifolia.*
A, Flowering shoot (West Greenland; July 12, 1884; slightly above nat. size). *B*, A shoot (West Greenland; May 18; a little above nat. size) with a terminal flower; at x the fresh green leaves begin. *C*, Branch from Norway (Finmark); July 7. *D*, Shows a lateral shoot which begins with an elongated internode. *E*, Plant from West Greenland, reduced (July 17); leaves very close-set. *F*, *G*. Diagrams to show the position of the leaves on the erect short shoots. *H*, *J*. Branches of the same plant (Norway; Aug.); internodes fairly elongated; *a*, limit of the year's-shoot, slightly reduced. (Drawn by E. W.)

The shoots branch irregularly; there is no principal bud. The erect shoots with short internodes rarely branch before flowering; the prostrate shoots give off branches which are also prostrate. Between loose moss the internodes of the shoots may become greatly elongated.

The leaves are foliage-leaves; scale-leaves do not occur.

The structure of the leaves will be described by Gallöe in the anatomical portion of this work. The shoots terminate during winter with fresh green, or sometimes reddish, leaves which do not decay until late in the ensuing summer. In a decaying condition the leaves may persist for many years (Fig. 25 *A*). During winter they serve as food for ptarmigans and other animals.[1]

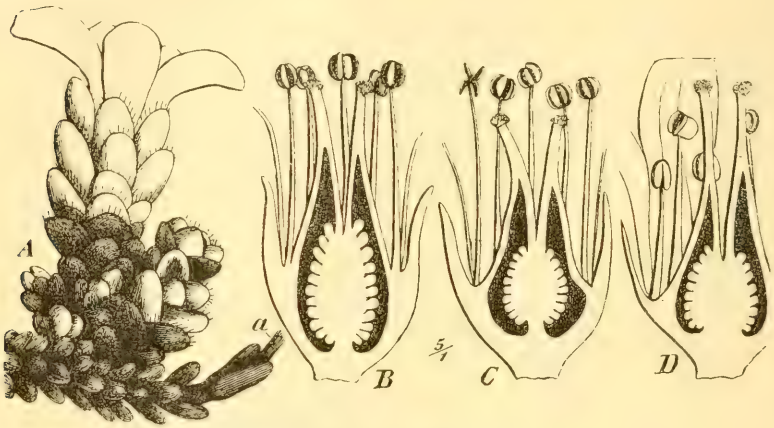

Fig. 25. *Saxifraga oppositifolia.*

From Greenland (*A*—*C*) and Norway: North Cape (*D*).

A, From Holstensborg (July 16, 1884); a dead stem bearing the fruit of the previous year is seen to arise at *a*; between the leaves of the previous year new shoots (the white ones) are being developed. *B*, Longitudinal section of a flower, in which all the stamens are erect and have their anthers open; the stigmas are ripe and stand quite close to the anthers or are even in contact with them. *C*, The stamens are erect, and are longer than the styles; all the anthers are open; germinating pollen-grains occur upon the stigmas. *D*, All the antisepalous stamens are open, but the antipetalous stamens are closed; pollen-grains are seen germinating upon the stigmas. (E. W., 1886.)

[1] During Nares's Polar-Expedition, on February 19, 1876, a hare was shot in 82°—83° N. lat., of which the following account was given: — "It is in excellent condition, and has been feeding on the leaves of the purple Saxifraga, willows and lichens. It is extraordinary how these animals find sufficient food with which to support life during the dark season, or how the buds of the plants can withstand such a low temperature." In the same work referring to Febr. 7, 1876, we read: — "On examining a plant of *Saxifraga oppositifolia* which has not been protected by any snow, and therefore has been exposed to the severest temperature, green buds were distinctly visible. In 1853 we killed a ptarmigan at Melville Island in February with green buds of willows in its crop.'

Seedlings have been described and figured by Lindmark. During the first year an epicotyledonary shoot is formed, about 5 mm. in height, and with short internodes; during the second year this becomes prostrate, its internodes elongate and it branches.

The shoots evidently may remain for several years in a vegetative stage until they terminate in a (usually) solitary flower. But they may also flower during the second year. The flowers which first expand often occur embedded between the foliage-leaves of the shoot (Fig. 25 *A*); the succeeding flowers may be raised into the air to a greater or lesser height, upon stems with elongated internodes (Fig. 24, *A*, *H*).

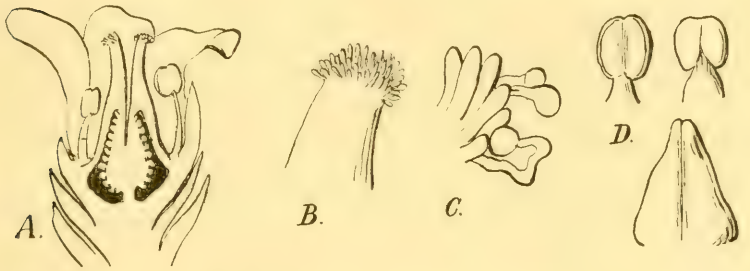

Fig. 26. *Saxifraga oppositifolia.*
A, A flower with very short stamens (about $^3/_1$). *B*, Stigma of the same flower, ripe, but without pollen (West Greenland; June 29, 1884). *C*, Germinating pollen from another flower. *D*, Stamens and pistil (about $^6/_1$) from a closed bud (West Greenland; May 18). (Drawn by E. W.)

The flowers pass the winter in a well-developed condition (Fig. 26 *D*). H. Jonsson found, in December, petals and stamens which were already coloured.

The diameter and the size of the flower vary on the whole widely. From Spitzbergen Ekstam reports 9—11 mm., and, exceptionally, 18—20 mm.; Andersson and Hesselman as much as 18; similar measurements were made in Greenland. This must evidently be connected not only with a difference of age, but also with the conditions of life.

The colour of the petals varies greatly. Some of the

flowers are pale red, others purple-coloured, or dull violet-red. White flowers also occur.

Scent. From Spitzbergen and Nova Zembla it is reported that the flowers have a strong scent (Holm, Ekstam); Nathorst even writes "almost sickening" in cases where the flowers occurred abundantly. I have not noted down any observation regarding the scent in Greenland.

Honey is often secreted abundantly by the base of the ovary. The flower is so widely expanded, that in rain or melting snow it may be filled with water. The flower is usually protogynous at first, but very soon becomes homogamous (Greenland, Scandinavia, Spitzbergen, Hortus Hafniensis, the Alps); I have found the styles bending outwards and the stigmas highly papillose, while the stamens were still short and had not opened one of their anthers. According to Lindman the stigmas ripen even before the flowers have fully expanded. At first the styles are longer than the stamens, but gradually the anthers of the latter attain the level of the stigmas and gather so closely around them that self-pollination takes place (Fig. 25 *B*, *C*, *D*).

The usual staminal movements of the *Saxifraga* occur here, but not with the usual vigour; Andersson and Hesselman even report that the stamens do not perform any movements at all (Spitzbergen), but remain sub-erect or even somewhat bent inwards. Lindman distinguishes between a form with larger flowers (see his Fig. 21 *A*, *B*) and one with smaller flowers (see his Fig. 21 *C*); the latter appears to be protogynous to a somewhat lesser degree. Transitional forms occur. The relation in length between the stamens and the pistils varies greatly; in flowers at the same stage of development, the stigmas may be situated above the anthers (Fig. 25 *D*), or at a level with them (Fig. 25 *B*), or at a lower level (Fig. 25 *C*). In the flower figured in Fig. 25 *D*, the styles are unusually long.

Protandry is evidently rare. Ekstam observed it in Nova

Zembla, and Dusén reports it in var. *Nathorsti* from East Greenland; he writes (p. 37): "Die vollkommen entwickelten Staubblätter ragen etwas über die Fruchtknoten; diese reifen später als jene." But immediately afterwards he reports protogyny.

Staminate flowers occur. Lindmark describes and figures such a flower, in which the pistil is very small, while the stamens are of the usual length. It did not set fruit.

Pistillate flowers, more or less closed, were found by Ekstam in Spitzbergen, late in summer. The stamens were almost rudimentary or were sterile. According to Schröter (p. 541) similar flowers were also found in the Alps by Schulz. The flower figured in my Fig. 26 *A* is perhaps a pistillate one.

Insect-visitors. Ekstam saw flies, and in Nova Zembla also many humble-bees, visit the flowers.[1] Lindman never saw insects visit the flowers, neither did I observe any in Greenland.

Self-pollination by contact of anther and stigma, is no doubt common everywhere in Arctic countries; it is also recorded from the Alps by H. Müller (p. 98). Stigmas and anthers are often found clustered close together in the middle of the flower, and frequently in intimate contact with each other (Fig. 25 *B*).

Fruit ripens in many places, in West and East Greenland, Iceland, the Færöes, Spitzbergen, Nova Zembla and Scandinavia. I found fruit set very early in Greenland, as early as June 28th, when the whole landscape around Godthaab was still very winterly, with snow even down to the sea; the fruit was in evident development.

According to Ekstam, 4- and 5-merous pistils occur.

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[1] "The occurrence of *Saxifraga oppositifolia* was an invariable evidence of humble-bees being present, and they were also seen in great quantities whirling over the plant-clusters as soon as the temperature was above + 4° C., and the wind not too sharp."

Saxifraga rivularis L.

Lange, Conspectus, pp. 61, 256. Rosenvinge, p. 679. Warming, 1886, p. 7, figs. 21—22. Lindman, p. 57, pl. II, fig. 22. N. Hartz, 1894, p. 37; 1895, p. 288. Jungner, p. 275. Ekstam, 1898, p. 17 (Spitzbergen). Abromeit, p. 34. G. Andersson och Hesselman, p. 29. Dusén, p. 33. Lindmark, p. 55, pl. III, figs. 8—14. Simmons, p. 76. Sylvén, p. 233.

Knuth, p. 449.

Primula-type, combined with runners and bulbs. The species has a very abbreviated, vertical rhizome with short internodes and many slender adventitious roots (Figs. 27 *A*; 28 *A*); when growing in damp moss the internodes become fairly elongated (Fig. 28 *C*); the rhizome dies away at the hinder end. At the base it bears sometimes several, sometimes a few dead leaves; and above these, a rosette of fresh, long-stalked foliage-leaves, which are palmately-reniform, 5—7 lobed, and set with glandular hairs (Fig. 27 *A*, *D*,; Fig. 28 *A*).

Runners. From the axils of the basal leaves may be seen to arise (as many as 5) pale, slender, horizontally-growing runners having on them glandular hairs (Fig. 27 *E*). They may attain a length of 6 cm., and generally bear scale-leaves which are sometimes succulent and may have small laminæ at their apices. The runners ultimately bend upwards, producing foliage-leaves and forming roots, and a new vertical rhizome arises (Fig. 27 *A*). The runners soon die. In some cases they are seen to be bent even somewhat downwards. Sometimes they bear foliage-leaves only. They may branch and form new runners.

Bulbils are also formed; they consist of a few, thick scale-leaves, which represent, in the main, the sheath of the foliage-leaves (Fig. 27 *B*; Fig. 28 *B*). The bulbils are formed in the leaf-axils of the rhizome simultaneously with, and in immediate proximity to, the runners (Fig. 27 *C*). According to Lindmark, who is a very careful observer and whose paper con-

tains valuable observations, bulbils may also arise terminally upon lateral shoots which bear foliage-leaves. The same is stated with regard to the runners, and I am able to confirm the statement (Fig. 28 *G*).

Foliage-leaves. The typical form and venation of the foliage-leaves are shown in Fig. 29 *A*, *B*. Entire (*D*) and nar-

Fig. 27. *Saxifraga rivularis*.

A, A runner from an older shoot which is in the act of expanding, bearing at first scale-leaves, and in the part turned upwards, foliage-leaves; at the point of transition between the horizontal and erect parts, roots are formed. *B*, Apex of a flowering shoot (from Spitzbergen; July 6, 1882; Nathorst). *C*, *D* (from West Greenland; Aug. 16, 1884), A bud with fleshy scale-leaves and a runner which at first bears similar leaves are both situated at the base of an erect shoot with elongated internodes which bears two foliage-leaves (the stalk of the lower, and the whole of the upper leaf is shown), a bract, and a flower. *E*, The apex of a runner; the covering of hairs, everywhere else omitted, is indicated here. (E. W., 1886.)

rowly-lobed (*C*) leaves occur. The venation is characteristic, the veins being curving and united at the apex. The leaf-base consists of a broad sheath which in form sometimes resembles the stipules of many *Rosaceæ* (Fig. 28 *D*).

The germination of the seed, and the seedlings are mentioned and figured by Lindmark. Ostenfeld also gathered seedlings in Iceland (Fig. 28 *E*, *F*). The primordial leaves form

a rosette. Lindmark thinks that the plants can flower in their second year.

Branching. Lateral shoots which, from the first, put forth imperfect foliage-leaves, are quickly developed into small

Fig. 28. *Saxifraga rivularis.*

A, From Disko (July 20, 1884). From the base of a shoot five white, rootless, slender runners are seen to proceed (slightly mag.). *B*, A runner; slightly mag. (Norway); the leaves *a* and *b* are fairly thick and fleshy; *c* and *d* have small entire laminæ; *e* a tripartite lamina. *C*, A slender, erect runner (West Greenland; Aug. 16, 1884); in the axils of the three leaves — which have been cut off — new runners have arisen (slightly reduced). *D*, A leaf with evident stipules. *E*, Seedling from Iceland; about $^2/_1$ (Ostenfeld; June 8, 1895). *F*, A cotyledon of it ($^8/_1$). *G*, A runner which terminates in a foliage-leaf and a bulbil. (Drawn by E. W., 1908.)

foliage-bearing rosette-shoots at the base of a flowering shoot. The greater number of the foliage-leaves which during the flowering-period, are seen at the base of the flowering-shoot often belong to lateral shoots. In unfavourable localities the lateral shoots become close-set, and the whole habit of the

plant becomes tufted. Abromeit mentions "very low, densely bushy plants, often only 15 mm. high," of Lange's f. *purpurascens*. I have also seen dense tufts, 2 cm. high, from Siberia.

Probably frequently a shoot remains only one year in the vegetative stage, and dies the second year, after flowering. But in unfavourable localities the shoots may remain vegetative several years.

The flowers are formed during the year previous to that in which they open. In specimens gathered by C. Ryder in West Greenland (Upernivik) from under the snow on July 18, 1887, the flowers had large anthers and a large pistil.

Sometimes only one, terminal flower occurs; sometimes a few-flowered inflorescence is developed.

The diameter of the flowers is small (5—8 mm., or sometimes, according to Ekstam, 10 mm.) because the petals are fairly erect (Fig. 30 *A*, *C*). Probably the flowers are always scentless. The petals are white, but red or dark-red examples occur (Lange writes regarding f. *purpurascens* "sepala atropurpurea; petala rubella." Andersson and Hesselman write (Spitzbergen): "sepals reddish-brown, petals white with a narrow band of reddish-violet colour; the gynoeceum reddish-violet." As is the case in *Saxifraga cernua*, irregular flowers occur, the petals on the one side of the flower being smaller than those on the other; this is seen especially in the young flower (Fig. 30 *C*).

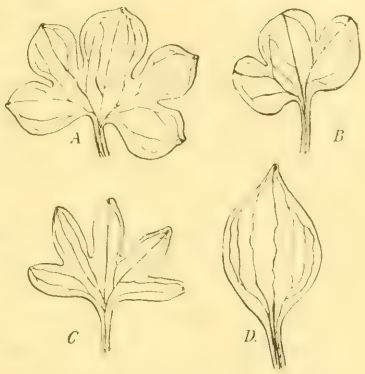

Fig. 29. *Saxifraga rivularis*. Forms of leaves from Greenland; slightly mag. *A*, A typical leaf. *B*, A similar leaf, but three-lobed. *C*, A narrowly-lobed leaf; *D*, An entire leaf. (Drawn by E. W., 1908.)

The stamens perform the usual movements, but less markedly, and remain on the whole fairly erect.

Slight protogyny or decided homogamy is the rule

(Greenland, Norway, Sweden). In the buds, the styles are erect or bent a little inwards, and the stigmas are slightly papillose. When the corolla begins to open, the stigmas are seen to be larger and more strongly papillose, and the anthers, then, stand closely around them (Fig. 32 *A*): they may at that time, still be closed, but there are also cases where I saw them evidently functional simultaneously with the stigmas. In 1886 (p. 8) I wrote: "I have noted down, e. g. from Sermersut at Sukkertoppen (July 5): even in the still half-closed flower the antisepalous stamens are open and the stigmas retain the pollen-grains."[1] The styles afterwards become more spreading, and as the anthers remain erect or even bend inwards over the middle of the flower, they will easily be able to come into contact with the stigmas. As a matter of fact, they are sometimes found in very close contact with them.

Self-pollination has been observed in Greenland (Warming), Norway (Lindman), Sweden (Lindmark). That it also causes true fruit-setting is evident from the fact that it is a constant rule for the inconspicuous and small flowers of these species to set fruit in regular succession one after the other; usually every flower on a plant sets fruit. This species, like *S. cæspitosa* and *S. oppositifolia*, is among the earliest flowering species; I found it fruiting on June 28th—30th in West

[1] Ekstam can scarcely have read this with care, as he writes "nach Warmings an Spiritusexemplaren gemachten Untersuchungen ist die Pflanze schwach proterogyn oder homogam." As he also speaks elsewhere of my observations as made upon alcohol-material, and evidently, for that reason, considers them less reliable, I repeat what I wrote on pp. 3—4 regarding the Ericineæ, namely that, as may also be seen from my statement cited above, I have made numerous observations on living material in Greenland and Norway, in many cases in the field, and made sketches of the flowers after this material, and that the spirit-material was only used for the verification of the forms, and as a basis for the figures. It is true, in some cases, that it was spirit-material alone which I had for examination, e. g. from Spitzbergen, but I am not aware that Ekstam has ever proved that many biological facts may not be observed on such material.

Greenland in very winterly surroundings, and as early as on July 10th Kornerup gathered it with ripe fruit in West Greenland. Ripe fruit is to hand from almost all our colonies in West Greenland. Bay, Kruuse and Hartz found ripe fruit in East Greenland. In the literature dealing with the subject, as well as in herbarium and spirit-material from many Arctic countries we find the same constancy in the fruit-setting (Iceland: Jonsson, Feddersen and Stefansson; Norway: Lindman; Sweden: Lindmark;

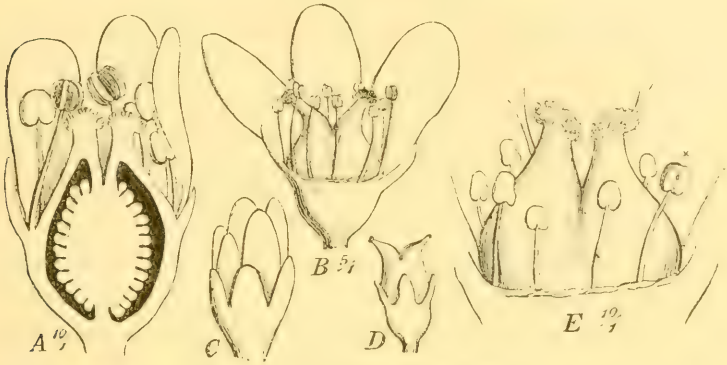

Fig. 30. *Saxifraga rivularis.*

A, In a flower with erect petals (and consequently rather closed, see Fig. *B*) the anthers of the antisepalous stamens and the stigmas are fully functional; the former are placed just above the latter (from Spitzbergen; July 6, 1882; A. G. Nathorst). *B*, An older flower, with expanded petals and spreading styles; here also the stigmas are in contact with the open anthers, which are filled with pollen (from West Greenland, Godhavn; July 20, 1884). *C*, Shows the obliquity which sometimes occurs in the flower. *D*, Young fruit (nat. size) from Spitzbergen. *E*, A flower (from Spitzbergen) with rudimentary stamens; the one marked × held a little pollen. (E. W., 1886.)

Lapland: Brotherus; Spitzbergen: Andersson and Hesselman; Siberia (the north coast): Kjellman; the Færöes and Jan Mayen: all who have collected material).

Insect-visitors. In Spitzbergen Ekstam observed flies visit the flowers.

I found the flowers from Spitzbergen to be somewhat smaller than those from Greenland, but otherwise they agreed entirely with the latter.

Pistillate flowers. On a specimen, gathered by Nathorst in Spitzbergen, with ordinary hermaphrodite flowers, a flower

(terminal?) was found with normal stigmas, but with stamens which were much shorter than usual, nine of which had no pollen in their anthers, and were decidedly sterile, but in the tenth there was a little pollen (Fig. 32 *E*).

According to Lindmark, the seeds do not germinate until the year after they have been formed, unless they are exposed to hard frost.

Saxifraga stellaris L.

Lange, Conspectus, pp. 60, 256. Rosenvinge, 1892, p. 678. Th. Holm. p. 51, pl. X, figs. 4—7. Warming, 1886, p. 10, fig. 23. Lindman, p. 59, pl. III, fig. 26. Ekstam, 1894 b, p. 426; 1897, p. 131; 1898, p. 12. G. Andersson och Hesselman, p. 23. A. Cleve, p. 48. Dusén, p. 32. Lindmark, p. 36, pl. II, figs. 4—17. Abromeit, p. 33. Skottsberg, p. 16. Sylvén, p. 230. Simmons, p. 69. H. Müller, p. 90. Günthart, 1902, p. 73. Knuth, p. 447.

Observations and alcohol-material from: — West Greenland (Warming, Th. Holm, Rosenvinge, N. Hartz, C. Ryder, Ostenfeld: Sukkertoppen, Egedesminde, Upernivik, Godthaab, Holstensborg, Frederikshaab, Kristianshaab); East Greenland (P. Eberlin: Dronning Louises Ø, Nunatsuk). Nova Zembla (Th. Holm). The Færöes (F. Börgesen: Kirkebö, 1000 feet). Norway (Warming, Kindberg: Tromsö, West Finmark, Dovre). Sweden (Bohlin: Härjedal; Forssell: Saltdal).

A herb of the *Primula*-type. It has a short (one to a few cm. long) rhizome, vertical or slightly oblique (Fig. 31 *A*, *B*, *F*). This dies away gradually at its lower end, so that vegetative propagation takes place by the lateral shoots becoming independent. The rhizome lives scarcely more than 2—3 years; the adventitious roots are slender and numerous. The primary root can live at least 2 years, and is found even on flowering specimens (Lindmark). The length, branching, etc. of the rhizome varies according to the diverse habitats (cf. Lindmark).

The foliage-leaves are in a rosette, but are fairly erect (Figs. 31, 32). Where the rhizome grows between moss, the

internodes are elongated. Scale-leaves are absent. The shoots may remain one or several years in a vegetative stage, before they terminate in an inflorescence.

During winter, fresh foliage-leaves may be met with, but they wither quickly during the second year. According to

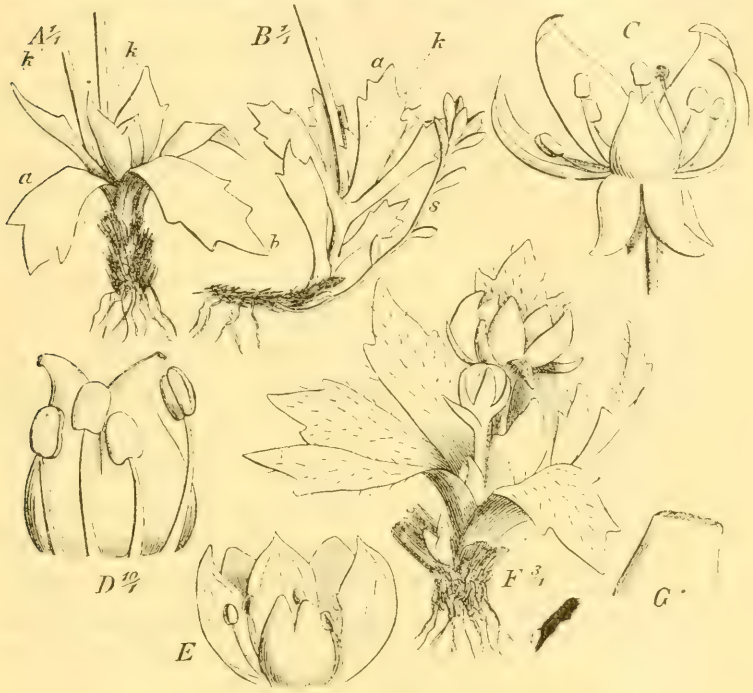

Fig. 31. *Saxifraga stellaris* L.

A, Basal portion of a plant from Sukkertoppen (Aug. 16, 1884); *k'* is the shoot axillary to the uppermost foliage-leaf *a*; it bears an inflorescence and one foliage-leaf; *k''* is the shoot axillary to the leaf *b*, which is next below; it is the principal shoot, i. e. next year's rejuvenating shoot. *B*, The principal shoot is subtended by *a*, its first leaves are indicated by *k*; *s* is a runner. *C*, Protandrous flower from Alten. *D*, Pistil and anthers of a protogynous flower from Åreskutan. *E*, Protandrous flower, with short stamens and erect petals (from a wet ravine at Nenese, East Greenland; Sept. 4, 1884; P. Eberlin). *F*, forma *acaulis* from Åreskutan (July 25, 1884; leg. O. Juel). *G*, Apex of style with stigma. (E. W., 1886.)

Lindmark the plant, especially in the higher regions of Scandinávia, turns more or less red in colour.

The branching. The rhizome may branch fairly freely, so that a dense tuft is formed. The most vigorous shoot occurs

in the axil of the uppermost leaf of the rosette; or, in case an inflorescence is developed in this, then in the axil of the leaf which is the next below (see Fig. 31 *A*, *B*); its leaves expand even during the flowering-period of the parent shoot. A few other shoots, usually 1—2, are developed in basipetal succession from the axils of the two next lower leaves of the rosette.

On older rhizomes, according to Lindmark, small buds occur which do not develop. All the branches begin with foliage-leaves, but when the plant grows in moss these become small and less perfect (Fig. 31 *B* at *s*). Small runners may occur (Fig. 31 *B*); they bear very small, entire leaves, and appear to be developed only under certain conditions, viz. in deep damp moss. The time for their flowering depends on the prevailing conditions (Lindmark).

Fig. 32. *Saxifraga stellaris* f. *acaulis*.
From Strömö (the Færöes), at 1000 feet above sea-level; about $^2/_1$. (June; leg. F. Börgesen).

The germination of the seed, and the seedlings have been described and figured by Lindmark. During the year in which germination takes place a leafy shoot with rather short internodes is developed which, like all the other shoots, passes the winter with its buds open. The seeds do not germinate until the year after they ripen.

The inflorescence is terminal on a long leafless peduncle. The uppermost lateral shoot sometimes flowers simultaneously with the parent shoot, and with or without a rosette of foliage-leaves (Fig. 31 *A*). In unfavourable localities the inflorescence remains sessile among the leaves of the rosette (f. *acaulis*; Fig. 31 *F*, Fig. 32).

Saxifraga stellaris f. *comosa* Retz. In the regions of the extreme north, a form *comosa* occurs, upon which only the terminal flower, or at most only a few normal flowers, are fully developed, and instead of flowers bulbils occur, far more abun-

dantly, indeed, than do the flowers on the principal form (Fig. 33 A). The bulbils consist of small, green, close-set rosettes of leaves which are lateral shoots of the 1st and 2nd order, the branches terminating either blindly or in a rudimentary flower. The bulbils are borne in the axils of the bracts. In the axils of the rosettes, other small rosettes are developed (axes of 2nd and perhaps higher order) so that the bulbils become compound shoots (see Th. Holm: Pl. X, Fig. 5; and my figure 33).

In 1886 I expressed doubt as to how far they fell off and germinated; but that they do this has since been recorded by Andersson and Hesselman, according to whom, in Spitzbergen, they begin to fall in August; by Lindmark, who has given good

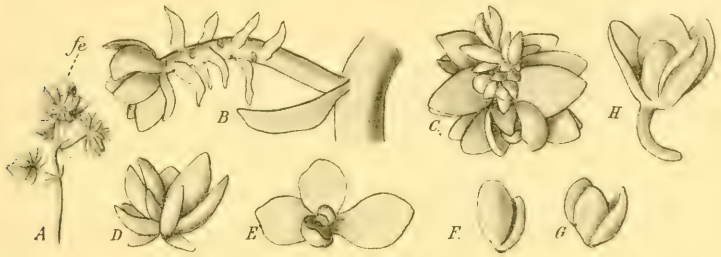

Fig 33. *Saxifraga stellaris* f. *comosa*.
A, A branch of an inflorescence; *fe*, the terminal flower (mag. 1½). *B*, A bulbil; most of its lateral shoots have fallen off. *C, D*, Bulbils; the leaves are seen to be partially opposite, the leaf-pairs representing the first leaves of shoots. *E*, A young bulbil, the leaves have been spread out. *F, G*, Small detached bulbils. *H*, A germinating bulbil. (E. W.)

figures of germinating specimens; and by Ekstam and Kerner; it has also been observed by Porsild, who like Lindmark found them even developing roots while they where still seated upon the parent plant (June 30, 1892); Fig. 33 *H*. These bulbils had lived through the winter in a fresh green condition.

All the observations indicate that this form is an adaptation to the extreme Arctic climate. Lindmark even writes: "there, where the principal form ends, *comosa* begins." In the regions of the far north (Spitzbergen and northernmost Greenland) it is the only form met with, or the most common; but the further we proceed southwards, the more common is the flower-bearing

form; and in central Scandinavia, and in the Alps, that is the only one which occurs, or at least, the most common.

The flowers are 6—9 mm. in diameter. Scent appears to be absent, but honey is secreted by the base of the entirely superior ovary, which I found to be greenish in Greenland, while according to H. Müller it is "purple-coloured" in the Alps. The honey is quite unprotected.

The petals are ovate-lanceolate with short claws, pointed at the apex, white or slightly yellowish-white in colour, with two decidedly greenish-yellow, or ultimately pure yellow, spots at the base. At first the petals are rather erect (Fig. 31 *E*, *F*), then they expand in a more stellate manner, while the sepals are turned right back (Fig. 31 *C*). I, also, observed the want of symmetry in colouration mentioned by H. Müller and Lindman, but did not find it so strongly marked. The anthers are usually of a red colour, which may be called decidedly yellowish-red, or by others purple-red, carmine-red, or minium-red.

Protandry. I found the flowers to be distinctly protandrous (in Norway), and this has also been recorded by others (Lindman, Ekstam (Nova Zembla), Lindmark, H. Müller, Günthart). Günthart states that the anthers usually begin to open even in the bud; according to him, protandrous flowers become afterwards homogamous, so that self-pollination becomes possible, and often takes place at the end of the flowering period. The stigmas are remarkably inconspicuous; they are neither of the very common form, with large papillæ; nor are they smooth and glistening, as in *S. nivalis*, and *S. hieraciifolia.* At first, the apices of the carpels are gently rounded and quite smooth (Fig. 31 *C*, *E*); when the stigmas are fully developed, a small, rough, somewhat glistening flat surface covered with small papillæ (Fig. 31 *G*) may be seen at each apex. The carpels are sometimes quite open, if viewed from the ventral side.

Homogamy. The flowers were found to be almost homo-

gamous in Scandinavia also (Lindman, Ekstam), with possibilities of self-pollination.

Protogyny. A flower gathered by Jcel in Sweden (Åreskutan; July 25) appeared to be protogynous (Fig. 31 *F*). The stigmas were distinctly ripe, but all the anthers were closed (Fig. 31 *D*); the same was the case with specimens from Hærjedalen (Sweden).

Regarding the specimens from Greenland, I have no notes on living specimens, but the flowers appear to agree closely with those from the north of Norway, and to be protandrous like them. The one from East Greenland, shown in Fig. 31 *E*, is evidently decidedly protandrous; all the anthers were open except one, and the stigmas were unripe; but otherwise it appears to differ somewhat, in its shorter stamens and small pollen-grains, which seem, however, to be quite normal. The petals were only slightly longer than the sepals, but the flower is evidently still very young.

Other specimens from the east coast of Greenland (gathered by Eberlin) appeared to be either homogamous or protogynous. Self-pollination must be able to take place, as the anthers were lying across the stigmas.

A forma *cryptopetala*, with petals smaller than the sepals, making the flowers very inconspicuous, and scarcely to be distinguished from the leaf-rosettes, is mentioned by Abromeit.

Pistillate flowers occur in East Greenland. In a specimen (gathered by Eberlin, Aug. 11, 1883) the antisepalous stamens were quite transparent and empty, while the pollen-grains in the antipetalous stamens were shrunken and abnormal.

A trimerous pistil often occurs in the terminal flower of the inflorescence (Greenland and Scandinavia), and this flower may sometimes be 6—7- or 8-merous instead of 5-merous.

Fruit is set in West, South and East (Angmassalik) Greenland, in Scandinavia, Iceland (where it ripens), the Færöes, and in Arctic America (King William's Land).

Saxifraga tricuspidata Retz.

Lange, Conspectus, p. 63. Rosenvinge, 1892, p. 679. Warming, 1886, p. 22, fig. 26. Abromeit, 1899, p. 35, pl. V, fig. 3. Günthart, 1902, p. 75. Simmons, 1906, p. 66.

Material in alcohol, and observations on living plants from West Greenland (Godhavn, Godthaab, Upernivik and Holstensborg) by Rosenvinge, Warming, Th. Holm and C. Ryder.

This plant has a tendency to become a sub-shrub. The ascending stems may attain a length of as much as 15—20 cm.

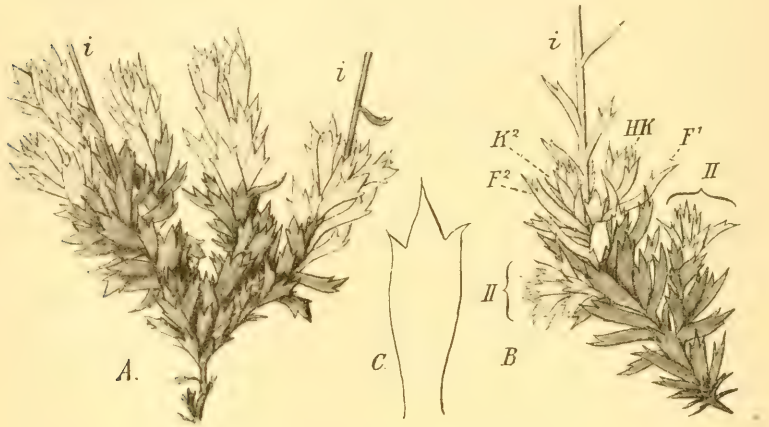

Fig. 34. *Saxifraga tricuspidata.*
A, From Upernivik (May 10, 1887; C. Ryder), from a spot bare of snow (about nat. size); *i*, *i*, two old inflorescences. *B*, From West Greenland (July 11, 1884); *i*, floral stem. *HK*, the principal bud; F^1, its subtending leaf; F^2, the leaf below it, with its axillary shoot K^2. *II*, *II*, two older lateral shoots (slightly reduced). *C*, Leaf, mag.
(Drawn by E. W., 1908.)

They grow in loose tufts, which no doubt in most cases have only one strong root, the primary root. The adventitious roots are weak and few in number; tufts, however, are sometimes met with which by centrifugal growth, as in certain lichens, become dead in the middle, while the periphery keeps on growing in a circular or semi-circular form; in this case it is no doubt only the numerous, slender, adventitious roots, which nourish the plant.

The vegetative shoots bear only foliage-leaves, which are

often more or less dark-red in colour. Scale-leaves are absent, but the branches bear, at first, entire foliage-leaves, and only higher up do the characteristic three points appear on the leaves (Fig. 34 C). In West Greenland, Vanhöffen found a form *subintegrifolia* Abrom. (l. c. Pl. V, Fig. 3) of which almost all the leaves were entire.

The leaves are seated very closely together upon a long, slender stem; sometimes a shoot is developed which has longer internodes.

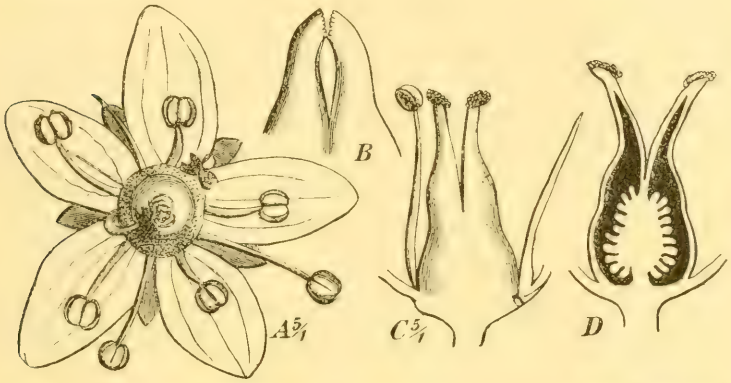

Fig. 35. *Saxifraga tricuspidata.* (From Holstensborg in West Greenland.) *A*, A flower in its first stage of development; two antisepalous stamens are bending over the middle of the flower, and have their anthers open; the stigmas are in the same stage of development as those shown in Fig. *B*. *C*, From a flower, the stigmas of which are functional; there is already pollen upon them. *D*, Longitudinal section of pistil at a somewhat later stage of its development. (E. W., 1886.)

The leaves remain green throughout one winter, but stay upon the branches a long time after death, colourless or black (Fig. 34 *A*, *B*). During winter (May 10, 1887), at Upernivik, in places bare of snow, judging from the material gathered by C. Ryder, the leaves are more erect (Fig. 34 *A*); during summer they are more spreading, and at that time the young leaves pass gradually into the old ones; often also the young leaves are red-coloured, as are those that have outlived the winter.

The branching. Below the terminal inflorescence one to three new shoots are developed in the upper leaf-axils, but

not always in the three uppermost; the uppermost shoot is the most vigorous, the others are weaker in basipetal succession (Fig. 34 *B*).

The shoots may pass several years in a purely vegetative condition before flowering begins.

The flowers and the inflorescences droop before opening (Fig. 36 *A*), but are erect during expansion. The diameter of the flower is 9—11 mm.

The petals spread out in a stellate manner (Fig. 35, 36 *B*); they are oval and have three veins (Fig. 36 *D*). The colour is evidently rather variable. I have noted and figured them as pale yellow, or whitish yellow with many small reddish-yellow spots which are darker the closer they occur towards the apex, where they may become almost purple. But other observations have also been recorded (cf. Abromeit). According to Vanhöffen there are two varieties, characterised by their different colour; the more common is white-flowered, with yellow or purple dots on the petals, which are long; the other, which is smaller, has distinctly yellow flowers with a few yellow, or more rarely red, dots.

Honey is secreted abundantly by the thick yellow base of the ovary (Fig. 35 *A*). It occurs in numerous small drops, even before the anthers open, and the secretion is continued for a very long time, even in old flowers. Scent was not noticed by me. Insect-visitors I did not observe.

Protandry occurs, but often not to any marked degree, and sooner or later homogamy usually ensues. The stamens perform the ordinary movements; first the antisepalous stamens bend forwards (Fig. 35 *A*), then the antipetalous; both kinds of anthers may be found simultaneously in the middle of the flower above the still unripe stigmas. Then they bend outwards, even if all the pollen-grains have not been shed. The styles bend outwards and the stigmas usually ripen before all the antisepalous anthers have opened. Homogamy lasts through-

out the greater part of the life of the flower. In cultivated specimens in Switzerland, Günthart observed the same order of development; autogamy always ultimately set in.

Self-pollination appears to take place. In Fig. 35 *C* the styles are somewhat spreading and the stigmas ripe; 1—2 antipetalous stamens were still erect and had their anthers close to the stigmas. None of the flowers with well developed stigmas and far-spreading styles (Fig. 35 *D*) had their anthers close to the stigmas.

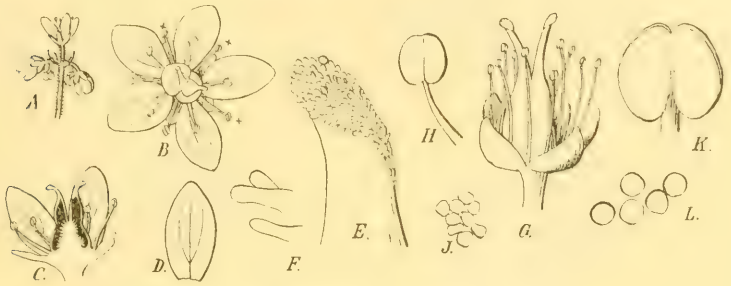

Fig. 36. *Saxifraga tricuspidata.*

A, Inflorescence; somewhat reduced. *B*, Small flower (about 3/1) from West Greenland (Aug. 5, 1884); the anthers of three of the stamens are open. *C*, The same in longitudinal section. *D*, Petal of the same. *E*, *F*, Style and stigmatic papillæ of the same. *G*, A pistillate flower from West Greenland. *H*, *J*, Stamen and pollen-grains of the same. *K*, *L*, Stamen and pollen-grains of a hermaphrodite flower, magnified as *H* and *J*. (Drawn by E. W., 1908.)

Fruit usually ripens in West Greenland. Parry gathered ripe fruit even at Duke of York Bay.

Forma *micrantha* Sternb. Pistillate flowers. A small-flowered form approaching this, was found at Holstensborg (July 13). Another (Aug. 5) is shown in Fig. 36 *B*—*F*. The stamens are unusually short, and the anthers very small. Three of the anthers (marked ×) were open and appeared to be normal. The stigmas were normal and one pollen-grain occurred upon them.

The form shown in Fig. 36 *B*—*F* appeared to be on the point of becoming pistillate. This is more decidedly the case with the form shown in Fig. 36 *G*—*J*, the anthers of which were unusually small, not open, and filled with angular, and evidently not normal, pollen; for comparison, the anther and pollen of

an ordinary hermaphrodite flower has been figured (Fig. 36 *K*, *L*), with the same magnification. Also Günthart found specimens "with extremely small stamens."

I found trimerous pistils in some terminal flowers.

Chrysosplenium alternifolium L. et var. **tetrandrum** Lund.

Warming, 1886 b, 3. Lindman, p. 56. Ekstam, 1897 a, p. 135. Andersson and Hesselman, p. 31. Simmons, p. 59. Silén, p. 125. Sylvén, p. 233, pl. II.

Knuth, 1898, pp. 453, 455.

Chrysosplenium alternifolium L. var. *tetrandrum* Lund was established in 1846 by N. Lund in Norway. Th. Fries (1858)

Fig. 37. *Chrysosplenium alternifolium* var. *tetrandrum*.
A, A runner terminating in a flowering shoot; about nat. size (Spitzbergen; June 25, 1882; Nathorst). *B*, A leaf from the same plant (mag.). *C*, Basal leaf from a cultivated specimen mag.). *D*, Leaf from one of the lower branches of an inflorescence; the venation, on the whole, resembles that of several of the *Saxifragae* (see Fig. 29). (Drawn by E. W.; 1908.)

regards it as a distinct species, *Ch. tetrandrum*. According to Simmons it is connected with the principal form by intermediate forms, and he agrees with Franchet in considering it a variety (Monographie du genre Chrysoplenium, Nouv. Archives du Museum, Ser. 3, X, 1890, p. 107). It should be regarded as a smaller and self-pollinating form of *C. alternifolium*, adapted to Arctic conditions of life.

The material I have had for examination was partly spirit-material from Spitzbergen, gathered by Nathorst, and partly living specimens, which I observed in the Hortus Bergianus (Stockholm).

The rhizome is creeping and has many adventitious roots which are arranged without order upon the internodes (Fig. 37 A). It branches, and produces runners which bear scale-leaves. The runners proceed principally from the base of the ascending stem. The reason why it remains more tufted and crowded than does *C. alternifolium* in temperate climates, should probably be sought in the fact that its runners are generally shorter than are those in our plants.

The rosette-leaves are long-stalked foliage-leaves (Fig. 37). From the axils of these also, runners are given off. Vegetative propagation takes place by the runners becoming independent.

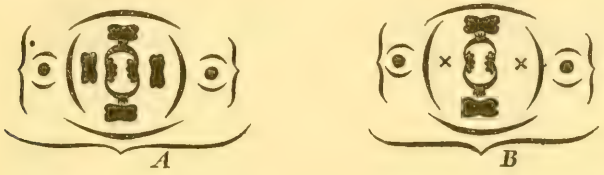

Fig. 38. *Chrysosplenium alternifolium* var. *tetrandrum*.
Diagrams of a complete (*A*) and of a diandrous flower (*B*) with the adjacent parts of the inflorescence (nat. size). (E. W., 1886.)

In the diagram of the flower shown in Fig. 38, the different parts are seen arranged in 5 alternating pairs. The two lateral stamens are often aborted (Fig. 38 *B*), in which case they become smaller than the normal ones, and their anthers differ in form and may be quite transparent and pale (Fig. 39 *E*, *F*). In a more closely-investigated specimen it was observed that the pollen-forming cell-layer had begun to extend itself, but had stopped, even before the primary mother-cells of the pollen were developed (Fig. 39 *G*).

In the spirit-material which I have had for examination, the perianth-leaves were not spreading, but erect (Fig. 39 *A*—*C*); in the principal form, from Denmark, they are spreading, as shown in Fig. 40. The diameter of the flower is consequently greater in the latter form.

Also the inflorescence in the var. *tetrandrum* comprises fewer flowers.

Colour. Th. Fries states that the perianth-leaves are yellowish-green with brown dots. I found cultivated specimens (Hortus Bergianus) in which they were greenish. Scent is absent.

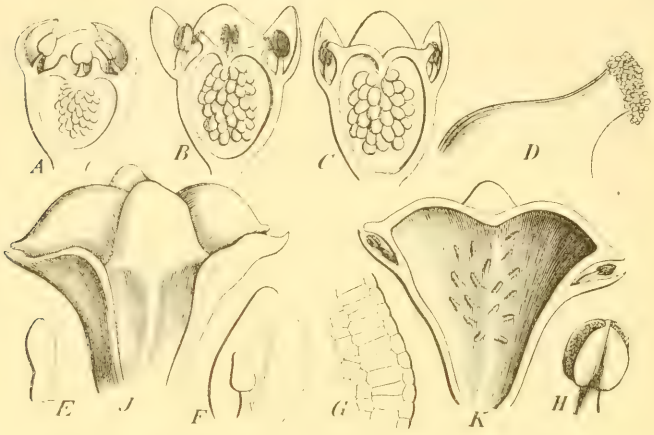

Fig. 39. *Chrysoplenium alternifolium* var. *tetrandrum*.
A, J, *K*, from cultivated specimens. *A*, Longitudinal section of a flower which is still almost a bud; the anthers are closed; the styles are short erect cones. *B*, Longitudinal section of a young, but fully expanded flower; the stigmas are partially in contact with the anthers which are shedding quantities of pollen upon them (*D* is from this same flower). *C*, A fertilised flower; the fruit- and seed-setting have begun; the free parts of the carpels are rising higher into the air, and the perianth-leaves are more closed. *D*, Style from *B* (more highly mag.); upon the stigmas are seen numerous pollen-grains. *E*, *F*, Sterile anthers, the latter in connection with its perianth-leaf. *G*, Longitudinal section through a sterile anther. *H*, Normal anther (magnified as *E* and *F*). *J*, Fruit, not yet quite ripe. *K*, Longitudinal section of a similar fruit; the seeds have been removed, but the funicles only partially. (E. W., 1886.)

The large yellow honey-secreting area of the principal form is no doubt entirely wanting from var. *tetrandrum*. If honey is secreted it must be in a small quantity only. All these things result in the flowers being far less conspicuous than are those of the principal form. In younger flowers, the free part of the carpels in the middle of the flower is very slight, but as the flower grows older it becomes larger, the styles bending outwards (Fig. 39 *C*, *J*, *K*).

Homogamy is the rule; perhaps slight protandry may occur, as the anthers sometimes appear to open before the stigmas are ripe. Self-pollination is no doubt inevitable and very common; it takes place by the stamens being always somewhat bent inwards or erect (Fig. 39 *A—C*); and as the styles very soon bend outwards the stigmas come into direct contact with the anthers of the two outermost stamens. I have found so many pollen-grains upon the stigmas (Fig. 39 *D*), that this must be due to self-pollination. In Danish specimens of the principal form the styles are not so decidedly bent outwards, and I never observed the stigmas to be in direct contact with the anthers; also, this would be difficult, owing to the length and position of the different parts (Fig. 40).

Fig. 40. *Chrysoplenium alternifolium.* Flower in longitudinal section; the ovules have been omitted. (E. W.; 1886.)

Homogamy was observed, in the principal form, in Scandinavia by Lindman, and in Germany by H. Müller and Knuth. Near Kiel, Knuth found only homogamous flowers, and they were visited, for their honey, by many flies, which effect cross-pollination, but may also effect self-pollination; this latter may also be effected by other means.

Protogynous-homogamous flowers were found by Ekstam in Nova Zembla. Protandrous-homogamous flowers were also recorded from there by Ekstam.

Fruit-setting. Judging from the material at hand, fruit-setting in v. *tetrandrum* appears to take place so invariably that no doubt every flower sets fruit and bears quantities of seed, which, on account of the prevailing circumstances, we cannot doubt is due to self-pollination. Insect-visitors have not been recorded. The carpels have brown dots. The fruit is said to open before the seeds are entirely ripe.

On account of the styles being directed towards the two outer (median) stamens, it is these only, which will be instrumental in effecting pollination. The two lateral stamens will scarcely ever come into contact with the stigmas; they become useless organs, which may, perhaps, be connected with the fact that they sometimes become rudimentary.

Chrysosplenium alternifolium v. *tetrandrum* is the most reduced type among the *Saxifragaceæ*; here, as in other instances, there is correlation between this and the small size of the flower.

Summary.

As the more general results of the investigations given in detail above, the following points may be mentioned.

I. Structure of stem. The species belong to several growth-forms, viz. the following: —

A. To the *Primula*-type belong: *S. hieraciifolia*, *S. nivalis* and *S. stellaris*. They have, as is the case in many species of *Primula*, a vertical, sympodial rhizome, with leaves in a rosette. The primary root dies early, and numerous adventitious roots are developed. The inflorescence is borne upon a leafless peduncle. The age and length of the rhizome here, as in other instances, is evidently dependent upon the dampness of the soil; the damper it is, the quicker does the rhizome die away at the hinder end. The rejuvenating shoots occur in the axils of the upper leaves of the rosette, the most vigorous in the axil of the uppermost leaf, while the others are weaker the farther down they occur. Sometimes, in the axil of the uppermost foliage-leaf, a lateral, floral shoot is developed even in the year the parent shoot flowers; this relegates the uppermost rejuvenating shoot to the axil of the leaf next below.

B. Nearest to this type come: *S. cernua*, *S. rivularis*, *S. Hirculus*, and *Chrysosplenium*. Here, also, are developed vertical rhizomes with foliage-leaves in a rosette, but the *Primula*-type is less pronounced, and is combined with the development of bulbils or of runners with scale-leaves or imperfect foliage-leaves, and adventitious roots.

C. To the *Sempervivum*-type belong: *S. Aizoon* and *S. flagellaris*. The principal stem is vertical and bears a close rosette of foliage-leaves; it has many adventitious roots and dies away entirely after flowering. Lateral shoots arise from the leaf-axils in no fixed order, they run more or less horizontally along the ground for some distance and terminate in a new rosette. In *S. flagellaris* the runner is very slender and consists of a single internode; in *S. Aizoon* it is short and includes several internodes.

D. Species with "rhizoma multiceps," a many-headed rhizome, are: *S. groenlandica* and *S. tricuspidata*. Their primary root remains alive a long time, which should probably be correlated with the dry localities in which they grow (crevices of rocks and bare stony ground in fell-fields). The adventitious roots, which are few in number, are usually of little importance; vegetative propagation, by the lateral shoots becoming independent, therefore takes place either rarely or not at all. The principal rejuvenating shoot is usually developed in the axil of the uppermost leaf, and other lateral shoots occur in basipetal succession. The first foliage-leaves of the lateral shoots may become so fully developed, even during the flowering of the parent shoot, that most of the foliage-leaves of the shoot-complex consist of them.

E. To the *creeping-herb*-type belong: *S. oppositifolia* and *S. aizoides*. The shoots are prostrate, and have their internodes more or less elongated. There is no regularity as regards the situation of their branches; no principal rejuvenating bud occurs. The primary root appears to be able to live several — perhaps

many — years, especially in *S. oppositifolia*; in *S. aizoides* it undoubtedly dies more quickly, in the course of a few years; this feature should probably be connected with the greater dampness of the habitat. In both species adventitious roots occur, and vegetative propagation takes place by the shoots becoming independent. *S. oppositifolia* has a tendency to become a sub-shrub, as its stems become more woody than do those of *S. aizoides*.

II. The leaves of the vegetative shoots are in all the species foliage-leaves. Buds, protected by true scale-leaves, do not occur. Only in those species which have bulbils and runners, do scale-leaves occur. Sometimes several, sometimes a few, leaves remain alive and green (or reddish) during winter; the following species have been noted as evergreen: — *S. aizoides*, *Aizoon*, *cernua*, *groenlandica*, *Hirculus*, *hieraciifolia*, *nivalis*, *oppositifolia*, *stellaris*, and *tricuspidata*. But they are not evergreen to the same extent, and this is probably also dependent in part on the nature of the locality.

The old, dead leaves persist for a long time upon the stems of some of the species, especially upon those which belong to the driest habitats (e. g. *S. tricuspidata*, *S. groenlandica*, *S. oppositifolia*, and *S. Aizoon*).

III. The flowers are developed the year previous to that in which they open, in perhaps all the species. This has been observed in the following: — *S. groenlandica*, *S. hieraciifolia*, *S. nivalis*, *S. oppositifolia*, and *S. rivularis*.

They are so fully developed that both stamens and pistils are distinctly formed, but pollen is scarcely formed, nor are the ovules developed. *S. oppositifolia* is the most developed.

There is undoubtedly a causal connection between this and the fact that the vegetation-period of the plants is so short in Arctic countries: the flowering of the plants must as a natural consequence be placed in early spring to enable the seeds to get sufficient warmth to ripen.

IV. Staminate flowers occur rarely (*S. oppositifolia*), but pistillate flowers appear to be common in a great many species, e. g., in *S. aizoides*, *cernua*, *groenlandica*, *Hirculus*, *nivalis*, *oppositifolia*, *rivularis*, *stellaris*, and *tricuspidata*. I also observed them in cultivated specimens (Hortus Hafniensis) of *S. groenlandica*, *S. Cymbalaria*, *S. Rocheliana*, *S. moschata* var. *glandulosa* and, to all appearance, in *S. cotyledon*. The pistillate flowers are smaller than the hermaphrodite ones; stamens are always present, but are smaller than usual, the anthers especially being small; pollen-grains are sometimes developed, but smaller than usual, and imperfect. In some cases the anthers dehisce, in others they do not. It appears especially to be the terminal flower in the inflorescence which thus develops.

In some species, deformed flowers with small petals have been observed — in systematic works named "*cryptopetala*" — e. g. in *S. cernua*, *S. groenlandica*, and *S. stellaris*. In some cases the petals at the same time that they were becoming small, were in the act of developing anthers at their apices.

Other numbers in the flowers than the normal five with two carpels have been observed; for instance, 6 and 7-merous flowers in *S. cernua*. It is especially the terminal flower in the inflorescence which shows a tendency to increase in the number of the carpels (probably because that flower is better nourished and therefore becomes larger and has room for a greater number of carpels). Thus, trimerous pistils have been found in *S. aizoides*, *groenlandica*, *hieraciifolia*, *stellaris*, and *tricuspidata*, 4- and 5-merous in *S. oppositifolia*. The terminal flower in the inflorescence may also be seen to differ in another point from the other flowers, viz. in the fact of its being far in advance of the others in regard to development, e. g. in *S. Aizoon*, and among cultivated species, in *S. geranioides* and *rotundifolia*. In *S. Geum* I found the pistil of the terminal flower to be formed somewhat differently from

those of the other flowers, and in *S. cernua* the terminal flower is often the only one which is developed.

Irregular flowers occur in *S. cernua*, *S. oppositifolia* and *S. rivularis*.

V. Pollination. The flowers have colour, and honey is secreted by the base of the pistil; in some instances scent has been noted. Insect-visitors have been observed in several of the species in Spitzbergen and Nova Zembla, especially by Ekstam, and in the mountain regions of Northern Europe by Lindman, Silén, Skottsberg and Sylvén.

Protandry is so common in the genus *Saxifraga* that Engler (Bot. Zeitung, 1868, and in his "Monographie der Gattung Saxifraga") even gives it as a generic character; that is also one of the reasons why he refers *S. crassifolia* and other protogynous species to the genus *Bergenia*. The nine species of *Saxifraga* mentioned by H. Müller in "Alpenblumen" are also nearly all decidedly protandrous, some protogynous species are however mentioned (*S. muscoides*, *S. androsacea*, *S. Sequieri*), and one, viz. *S. oppositifolia*, oscillates between slight protogyny, slight protandry, and homogamy. To these Müller afterwards added *S. tridactylites* as protogynous, while Sprengel found it to be protandrous.

The above-mentioned Arctic species give further proof that protandry is not a generic character; true, it occurs most commonly, but, firstly, it appears usually to be somewhat slighter — at least than it is in many cultivated species which I have observed in the Hortus Hafniensis, almost all of which were decidedly protandrous; usually, they become very soon homogamous: I have observed protandry in *S. aizoides*, *Aizoon*, *cernua*, *groenlandica*, *hieraciifolia*, *Hirculus*, *nivalis*, *rivularis*, *stellaris* and *tricuspidata*, as also in *Chrysosplenium*. Secondly, the same species often varies, being either protandrous-homogamous, or homogamous from the first. *S. groenlandica*, *hieraciifolia*, *nivalis*, *rivularis*, *stellaris*, *tricuspidata* and *Chryso-*

splenium are homogamous or oscillate around homogamy; it is especially the small-flowered species, which are homogamous.

Protogyny occurs in *S. cernua*, *groenlandica*, *hieraciifolia*, *nivalis*, and *stellaris*, but usually slightly Most distinctly and decidedly protogynous is *S. oppositifolia*.

I may add that Asa Gray ("Notes on some North American Species of Saxifraga," in Proceedings of the American Academy, XX) states that most of the individuals of *S. peltata* have protandrous flowers; but that it is not rare to find some which are truly protogynous, and that the species shows a decided tendency to become gynomonoecious. In the Hortus hafniensis *S. peltata* is seen to be protogynous. Regarding *S. granulata*, Gaston Bonnier says: "On peut voir chez ce Saxifraga des fleurs presque mâles, des fleurs presque femelles, et en outre tous les intermediares." (Bulletin de la Soc. botan. de France, VI, 1884, p. 240).

The staminal movements are those usual in the *Saxifraga* (see, e. g. p. 174).

Self-pollination is evidently very common. The small-flowered species are all more or less distinctly self-pollinating. Among the larger-flowered, several are evidently distinctly self-pollinating, if not in the first stage of the flower, then somewhat later. In the Botanic Garden of the University of Copenhagen *S. groenlandica* is more distinctly protandrous than in Greenland; it is true that, in the latter place it is also decidedly protandrous, but there the flower soon becomes homogamous and self-pollinating. The possibility of self-pollination will most probably always ultimately occur by the flower becoming homogamous, and stigma and anthers approaching and possibly touching each other, e. g. in *S. Aizoon*, *cernua*, *flagellaris*, *groenlandica*, *hieraciifolia*, *nivalis*, *oppositifolia* and *Chrysosplenium*.

VI. Fruit-setting and seed-formation is common in many species everywhere in the Arctic countries, and rare or

even very rare in other species; the latter fact is distinctly in causal relationship to their abundant vegetative propagation. In the species in which this is very scarce — therefore, especially in the species belonging to the types D and E, but also in those of the types C and A — the seed ripens, although perhaps not every year in every locality; this therefore occurs especially in the following species: — *S. groenlandica*, *tricuspidata*, *oppositifolia* and *hieraciifolia*, but also in *aizoides*, *Aizoon*, *Hirculus*, *flagellaris* and *nivalis*. The species which either do not set seed at all or do so rarely, are those which by bulbils or similar means have an abundant vegetative propagation; therefore especially *S. cernua*, *rivularis* and *stellaris* f. *comosa*. The most interesting species in this connection is *S. stellaris* with its form *comosa* (see above pp. 218—220). For the rest, how abundant and common fruit-setting is, e. g. in *S. flagellaris*, *S. Hirculus*, and other species, requires to be more fully investigated.

4.

Saxifragaceæ.

2. The Biological Leaf-anatomy of the Arctic species of Saxifraga.

By

Olaf Galløe.

1910.

INTRODUCTION.

A biological-anatomical description of the Arctic species of *Saxifraga* must essentially have reference to the foliage-leaves, as they are the organs which most distinctly bear the impression of external factors in nature. The roots were less suitable for anatomical investigation in the material which has been within my reach. All the material which I have had for examination has been placed at my disposal by the director of the Botanical Museum in Copenhagen.

The literature of the subject does not contain much regarding the leaf-anatomy of the genus *Saxifraga*. Engler was the first to give a more exhaustive account of it in his monographic treatment of the whole genus (Breslau, 1872. See list of literature). He does not treat the individual species anatomically, but confines himself to a kind of comprehensive characterization, without entering more fully into the peculiarities of the different species. The genus is treated in very much the same way by Thouvenin (1890) and Leist (1890). (I have unfortunately been unable to have access to a paper by Waldner (Graz, 1885) on the "lime-druses" of the *Saxifragas*).

The first three works mentioned above give, therefore, only very scattered data regarding the species we are here considering, and treat them according to systematic principles, without discussing the connection between structure and biological conditions.

More exhaustive descriptions are given by Leist (1889), Bonnier (1894), Borgesen (1895), Lazniewski (1896). These works aim particularly at elucidating the relation between habitat and anatomical structure, — Leist and Lazniewski with regard to the Alpine, Borgesen with regard to the Arctic plants. Bonnier compares Alpine with Arctic specimens of the same species; among the many examples he gives, he mentions only one *Saxifraga (S. Aizoon)*. Freidenfelt (1904) occupies himself with the root-anatomy of a few species, considering them to a certain extent from a biological point of view. Holm (1885) mentions the anatomy of several Arctic species,

and I shall have occasion to refer to his work in the following pages. Lindmark (1902), also, has made a few anatomical observations on the subject.

It is beyond the scope of this paper to discuss more fully the contradictory conclusions which previous authors have considered might be drawn from their studies of Alpine plants; here it will suffice for me to give the names of the contending parties (Bonnier, Leist, Wagner and Lazniewski) in the list of literature, and also Stenstrøm who has, in a very comprehensive manner, studied and discussed the questions here under consideration. Quite recently Schroeter (1904—08) has published some valuable observations upon Alpine *Saxifragas*. The investigations of these authors have been taken into consideration only in so far as they have touched upon Arctic species.

Here we are only concerned with those Arctic species which have been partially investigated by Th. Holm and F. Borgesen. I shall not enter more closely into the general and comprehensive results which Borgesen gives in his paper.

The specimens investigated by me are the following: —

Saxifraga aizoides L. ..... p. 266
— *Aizoon* Jacq. ..... p. 280
— *cernua* L. ..... p. 242
— *Cotyledon* L. ..... p. 276
— *flagellaris* Willd. ..... p. 269
— *groenlandica* L. ..... p. 261
— *hieraciifolia* W. K. ..... p. 253
— *hypnoides* L. ..... p. 258
— *nivalis* L. ..... p. 250
— *oppositifolia* L. ..... p. 285
— *rivularis* L. ..... p. 246
— *stellaris* L. ..... p. 255
— *tricuspidata* Rottb. ..... p. 273

These belong to six different sections. Common to all the species is a leaf-venation which is either palmate or appears to have been derived from the palmate type even in such divergent forms as S. *aizoides* and *oppositifolia*, the relatively serrate and entire leaves of which, with regard to venation and form, are connected by gradually transitional forms (especially *S. tricuspidata*) with the palmate leaf of, for instance, *S. cernua*. Moreover,

hydathodes are present in all the species. Consequently, the principal form (the type) had probably palmately-veined leaves with hydathodes. Nearest to this type-form are the mesophytic species with large leaf-blades, distinct leaf-stalks and marked differentiation between palisade-tissue and spongy parenchyma (the sections *Boraphila*, *Nephrophyllum*, and *Dactyloides* in part); less close to the type are the more decided xerophytes, with leaf-rosettes, narrow leaf-blades, etc. (the sections *Trachyphyllum*, *Euaizonia*, *Porphyrion*).

The following is a list of the chief literature upon the subject: —

Bonnier: Recherches expérimentales sur l'adaptations des plantes au climat alpin (Ann. des sc. nat., VII sér., T. XX) 1895.

— Les plantes arctiques comparées aux mêmes espèces des Alpes etc. (Révue gén. d. bot., T. VI) 1894.

Børgesen, F.: Bidrag til Kundskaben om arktiske Planters Bladbygning (Bot. Tidsskrift, Bd. 19) 1895.

Engler, A.: Monographie d. Gattung Saxifraga. Breslau, 1872.

Freidenfelt: Der anatomische Bau der Wurzel etc. (Bibliotheca botanica, Heft 61) 1904.

Holm, Th.: Novaja-Zemlia's Vegetation, særligt dens Phanerogamer. (Dijmphna-Togtets zool.-bot. Udbytte, København, 1885).

Lindmark: Bidrag til kännedomen om de svenska Saxifraga-artens yttre byggnad. (Bihang till k. svenska Vet.-Akad. handl., Bd. 28, Afd. III, Nr. 2) 1902.

Lazniewski, W. v.: Beitr. z. Biol. d. Alpenpflanzen (Flora) 1896.

Leist: Ueber den Einfluss des alpin. Standortes auf die Ausbildung d. Laubblätter (Separat-Abdruck aus Mittheil. d. Naturf. Gesellsch. von Bern) Bern, 1889.

— Beitr. z. vergleich. Anat. d. Saxifragen (Bot. Centralblatt XLIII) 1890.

Norman, J M.: Norges arktiske Flora, II, 1895.

Rosenvinge, L. Kolderup: Andet Tillæg til Grønlands Fanerogam- og Karsporeplanter. (Meddelelser om Grønland, III) (separate copy) 1892.

Schroeter: Das Pflanzenleben d. Alpen. Zürich, 1904—08.

Stenstrom: Ueber das Verhalten derselben Arten in verschiedenen Klimaten etc. (Flora) 1895.

Thouvenin: Recherches sur la structure des Saxifragacées (Ann. d. sc. nat., sér. VII, T. II) 1890.

Wagner, A.: Zur Kenntniss des Blattbaues d. Alpenpflanzen etc. (Sitzungsber. d. Wiener-Akad., Bd. CI, Abth. I) 1892.

Warming, E.: Grønlands Vegetation. (Meddelelser om Grønland, Hefte XII) 1888.

1. *Nephrophyllum.*

The two species of this group which have been investigated agree in the following points: — (1) The leaves are stalked and palmately lobed, (2) the epidermis has undulating radial walls, (3) glandular hairs are present, (4) the cells of the spongy parenchyma are decidedly stellate (without a compact layer of tissue under the epidermis), (5) the hydathodes are exactly marginal, without a cavity and without secretion of lime.

The species differ most in regard to the thickness of the outer walls of the epidermis, and the more or less decidedly stellate form of the cells of the spongy parenchyma. The two species can easily be distinguished from each other by these features, while, however, their mutual relationship is very distinctly expressed in their anatomy. A key to their determination by their leaf-anatomy would be as follows: —

Outer walls of the epidermis: —

(a) thin (2—3 μ): *S. cernua.*

(b) irregularly thickened (as much as 8—10 μ): *S. rivularis.*

Glandular hairs: —

(a) long-stalked upon the upper, and short-stalked upon the lower surface: *S. cernua.*

(b) similar upon the upper and lower surface: *S. rivularis.*

Saxifraga cernua L. (Figs. 1 and 2).

This species according to Norman (l. c., pp. 303—04) is a decidedly Arctic plant which extends beyond the tree-limit 697 metres and upwards. Grows both upon flat and sloping ground, as commonly on the northern as on the southern side, more rarely on the eastern and western sides. It prefers cold and damp localities, among moss, along the banks of rivers, upon stones in rivers, etc., and must be characterized as decidedly hygrophilous.

The leaves are long-stalked, reniformly-palmately lobed

with 5—7 lobes. Each lobe terminates in a hydathode (Fig. 1 *A*). Along the margin and upon both surfaces glandular hairs occur, long upon the upper surface and short upon the lower (Fig. 2 *E.*)

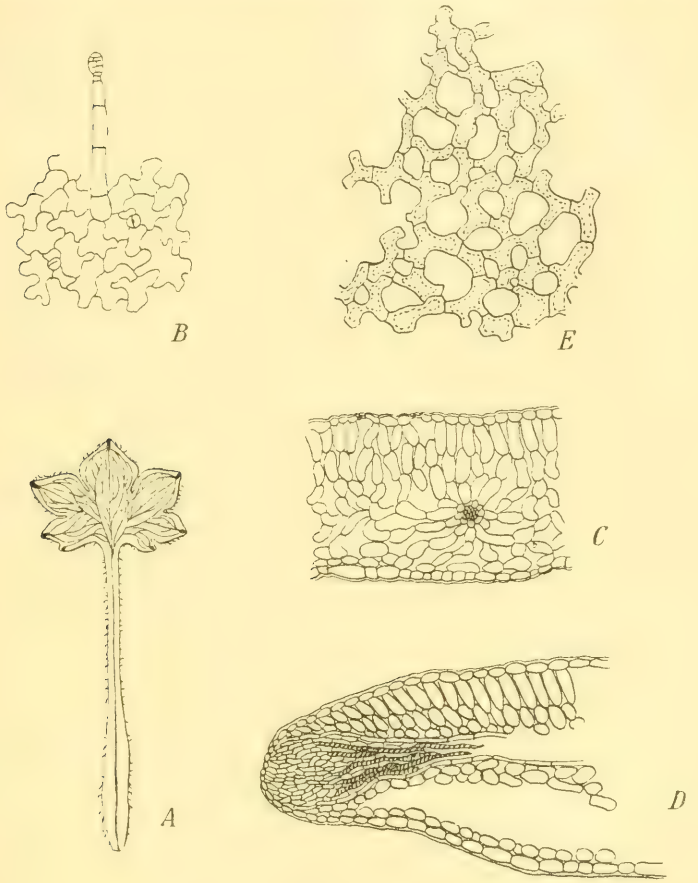

Fig. 1. *Saxifraga cernua.*
A (3/2), Leaf-form. *B*, Upper epidermis with a glandular hair. *C*, Transverse section of leaf. *D*, Longitudinal section of leaf-apex with hydathode. *E*, Spongy parenchyma. (*B*, *C*, *D* and *E* 50/1).

The epidermis of the upper surface consists of cells with undulating walls (Fig. 1 *B*), the lateral and outer walls of which are thin (2—3 μ). Cuticle is very slightly developed. The epidermis of the upper surface is provided with stomata which project above

the leaf-surface and also with scattered, long-stalked glandular hairs. Borgesen (l. c., pp. 225—26) states that the stomata are most numerous upon the upper surface, where there are 10 per unit of surface, while on the lower surface only 8.

The epidermis of the lower surface has even more strongly undulating walls; it is otherwise very slightly developed (as upon

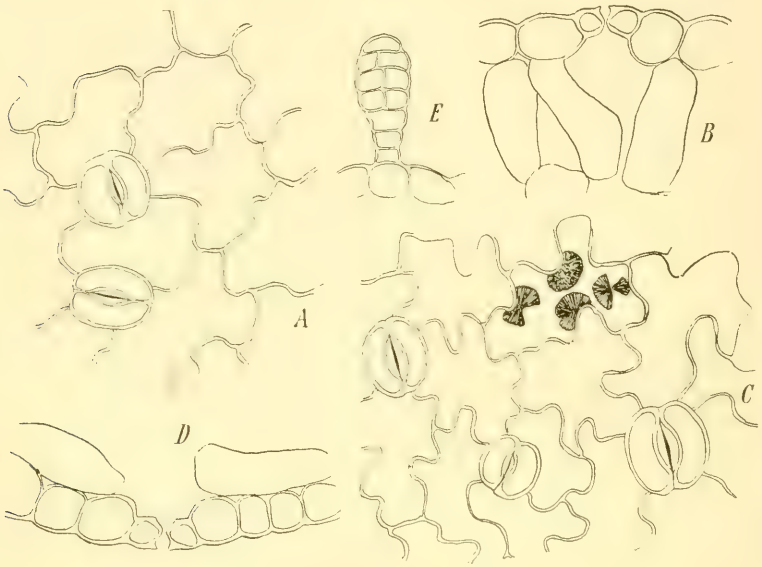

Fig. 2. *Saxifraga cernua.*
A, Epidermis of the upper surface of the leaf. *B*, The same in vertical section. *C*, Epidermis of the lower surface of the leaf (in a solitary cell several crystal-aggregates are seen). *D*, Lower epidermis in vertical section. *E*, Hair from the lower surface of the leaf ($^{282}/_{1}$).

the upper surface) and is provided with stomata, placed slightly above the level of the leaf-surface, and short-stalked glandular hairs exactly similar in appearance to those upon the margin of the leaves (Fig. 2 *E*).

The mesophyll is very loosely arranged, with large and numerous intercellular spaces (Fig. 1 *C*). The palisade-cells form indistinct rows and, in the greater part of the leaf, are placed almost vertically within the epidermis while towards the apex of the veins they are placed somewhat obliquely — a circumstance

which has been exhaustively discussed by Lazniewski (l. c.) in regard to rosette-plants and which we shall find again in the very decidedly rosette-forming species (*S. Cotyledon*, *Aizoon*, etc.). The 2—3 palisade-layers are differenced, but not very distinctly, from the cells of the spongy parenchyma, which are decidedly stellate (i. e. branched), long, and loosely arranged (Fig. 1, *E.*)

The veins are not accompanied by mechanical tissue, but are surrounded by a (usually one-layered) bundle-sheath of elongated cells devoid of chlorophyll (Fig. 1 *C*).

All the veins at the apices of the leaves terminate in a hydathode. The epithema is interwoven, and enveloped by the spirally thickened tracheids of afferent veins and is covered with a small-celled epidermis with water-pores. Lime-secretions were totally absent from the Arctic specimens examined by me. The surface of the epithema is convex and situated directly at the edge of the leaf-margin; a hydathode-cavity is absent (compare, *S. oppositifolia*, *S. Aizoon*, etc., the hydathodes of which open upon the upper side of the leaf-margin and have a cavity). Fig. 1 *D.*

The leaves of the bulbils are morphologically somewhat different; a gradual transition may be traced from entirely bladeless scale-leaves to bulb-scales with rudimentary leaf-blades which have entire margins, and ultimately to bulb-scales with a small three-lobed blade (the cells of which are devoid of starch-grains although the latter occur in quantities in the leaf-base).

The bulb-scales are without hydathodes. The cell-walls of the lower epidermis are almost straight; no stomata were found by me although they were found by Th. Holm (l. c., p. 47). The hairs are similar to those upon the lower surface of the foliage-leaves.

The cell-walls of the upper epidermis are straight, and there are no stomata. The hairs are similar to those upon the upper surface of the foliage-leaves.

All the cells of the mesophyll are alike, isodiametric and closely filled with starch-grains.

There is a solitary vein with a one-layered bundle-sheath devoid of starch.

The structure of the foliage-leaf and bulb-scale here described I found to be identical with that of the specimens from Mödruvellir in Iceland, and Egedesminde in Greenland.

As already mentioned, this species is hygrophytic in its choice of localities. Its anatomical structure is in distinct conformity therewith: Stomata (projecting above the level of the leaf-surface) on both sides; thin epidermis, — in short, no means of protection against excessive transpiration.

Saxifraga rivularis L. (Figs. 3 and 4).

Saxifraga rivularis L. is a decided mountain-plant which occurs most frequently on sloping ground, more numerously upon the shady than upon the sunny side. Probably grows usually in damp localities, and in the choice of its localities is almost exactly like *S. cernua* (Norman, l. c.).

The leaf is reniform and palmately-lobed, with usually 5 lobes, each provided with a hydathode at its apex (Fig. 3 *A*). Glandular hairs occur sparsely upon both surfaces.

The epidermis of the upper surface consists of large cells, which have slightly undulating walls and thin lateral and inner walls and irregularly thickened outer walls (Fig. 4). Cuticle thin. Stomata numerous and prominent. Glandular hairs are scattered over the whole surface, but are not abundant. Borgesen (l. c., p. 225) states that the stomata are most numerous upon the upper side, but yet he mentions (l. c., p. 226) having found 9 per unit of surface upon both the upper and lower surface.

The epidermis of the lower surface is almost exactly like that of the upper, but the cells are somewhat larger, and the walls more undulating (along the veins, however, to a less degree than outside them). (Fig. 4 *A, C.*)

The stomata here also are placed very slightly above the level of the leaf-surface; they are most numerous outside the veins (in the angles between the lobes), but are not entirely absent from along their length.

The mesophyll is exactly like that of *S. cernua*. What has been said above of the palisade-cells, spongy parenchyma and veins of the latter species will apply without any alteration to the

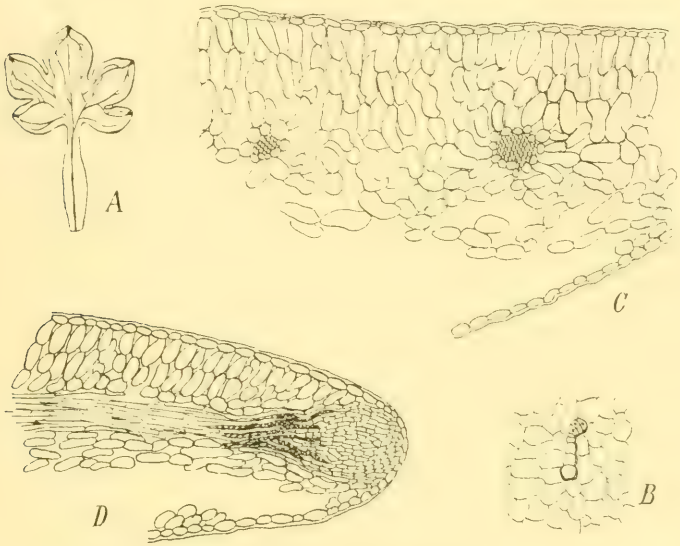

Fig. 3. *Saxifraga rivularis.*
A, (2/1) Leaf-form. *B*, Upper epidermis. *C*, Transverse section of leaf. *D*, Longitudinal section of tip of same with hydathode. (*B*, *C*, and *D* 50/1).

present species also. The palisade-cells in this plant also are oblique; Borgesen evidently did not observe this feature, neither does he describe the hydathodes; the latter are exactly like those of *S. cernua*. It is extremely interesting to note how the modes of life of these two closely-allied species are reflected, with such close correspondence, in the anatomical structure of their leaves.

The material upon which the description here given is based, comes from the following localities: — Jan Mayen (July 22,

1896), Mödruvellir (Iceland, May 19, 1889), Upernivik (July 18, 1886), Danmarks Ø (Aug. 1, 1892), Frederikshaab (June 8, 1888), Malersomiarfik (July 6), Nova Zembla and Tromsø (June 26,

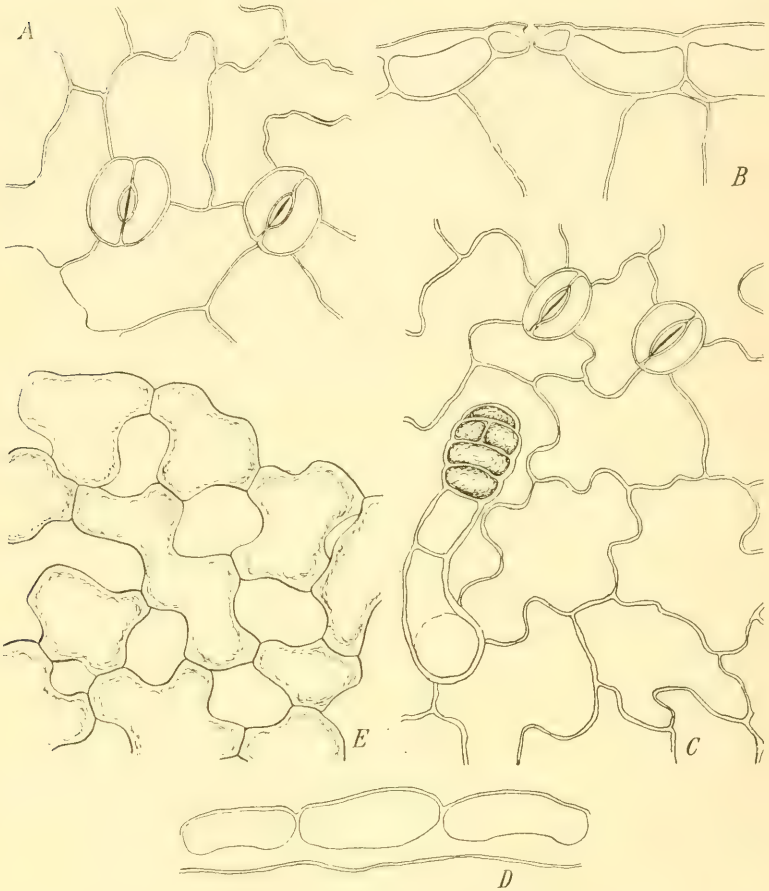

Fig. 4. *Saxifraga rivularis.*
A, Epidermis of the upper surface of the leaf. *B*, The same (transverse section). *C*, Epidermis of the lower surface of the leaf. *D*, The same. *E*, Spongy parenchyma. (*A*, *B*, *C*, *D*, and *E* $^{282}/_{1}$).

1885); therefore from Norway, Iceland, Nova Zembla, Greenland and Jan Mayen. In spite of the widely separated localities of the individuals they were all absolutely identical in regard to leaf-anatomy. The specimens which have been investigated

give no insight into possible seasonal differences; they were all collected between the end of June and the beginning of August.

Lastly, I may add, that I have examined numerous roots of this plant, without finding any kind of mycorhiza; but this also, no doubt, could scarcely be expected to be found.

2. *Boraphila.*

The three species of this group agree closely in the following features: — (1) Epidermis with undulating walls, (2) glandular hairs, (3) marked difference between the palisade-tissue and the spongy parenchyma (the spongy parenchyma varying from cells which are slightly branched, but arranged in irregular meshes and rows, with larger intercellular spaces (*S. stellaris*) — to much branched ("stellate") cells in the species *S. nivalis* and *S. hieraciifolia*; compact spongy parenchyma immediately beneath the epidermis does not occur), (4) hydathodes exactly like those in the section *Nephrophyllum*. The differences are as follows: —

Hairs: —

Two kinds (i. e. both glandular hairs and marginal non-glandular hairs): *S. nivalis* and *S. stellaris*.

Glandular hairs only: *S. hieraciifolia*.

Spongy parenchyma: —

(1) very loosely arranged, consisting of unbranched and branched cells, in rows of irregular length, the main direction of which is parallel to the longitudinal axis of the leaf: *S. stellaris*.

(2) all the cells of the spongy parenchyma branched: *S. hieraciifolia* and *nivalis*.

It can therefore be seen that the leaf-anatomy of this section corresponds closely with that of the section *Nephrophyllum*. It is in reality impossible, on the basis of our knowledge

of the species of which the investigation is here recorded, to point out any anatomical difference which characterizes the whole of the one section in contradistinction to the whole of the other.

Saxifraga nivalis L. (Figs. 5 and 6).

Saxifraga nivalis L. occurs far above the tree-limit in Arctic regions, where (according to Norman) it usually grows on

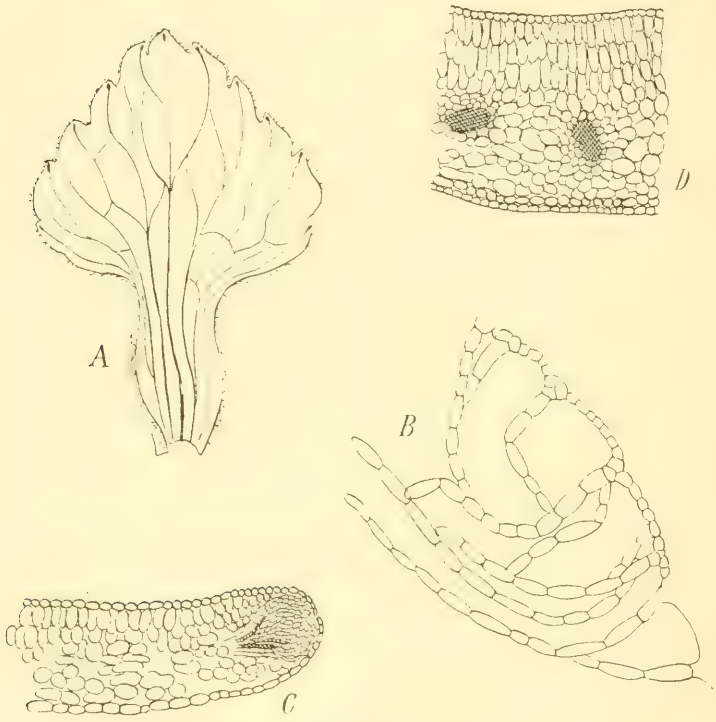

Fig. 5. *Saxifraga nivalis.*
A (2/1), Leaf-form. *B*, Hairs from leaf-margin. *C*, Longitudinal section of leaf with hydathode. *D*, Transverse section of leaf. (*B*, *C*, and *D* 50/1).

sloping ground, three times more commonly on the sunny side than on the shady side; it usually grows in dry localities, more rarely in damp. M. Porsild informs me verbally that in Greenland it is found among damp moss and upon cliffs wetted by spray. The plant according to my judgement is fairly distinctly

mesophytic in its anatomical structure. The leaves are cordate, with a hydathode at the apex of each tooth. (Fig. 5 *A*.)

The epidermis of the upper surface consists of cells which have undulating walls and thin (about 2μ) lateral, inner and

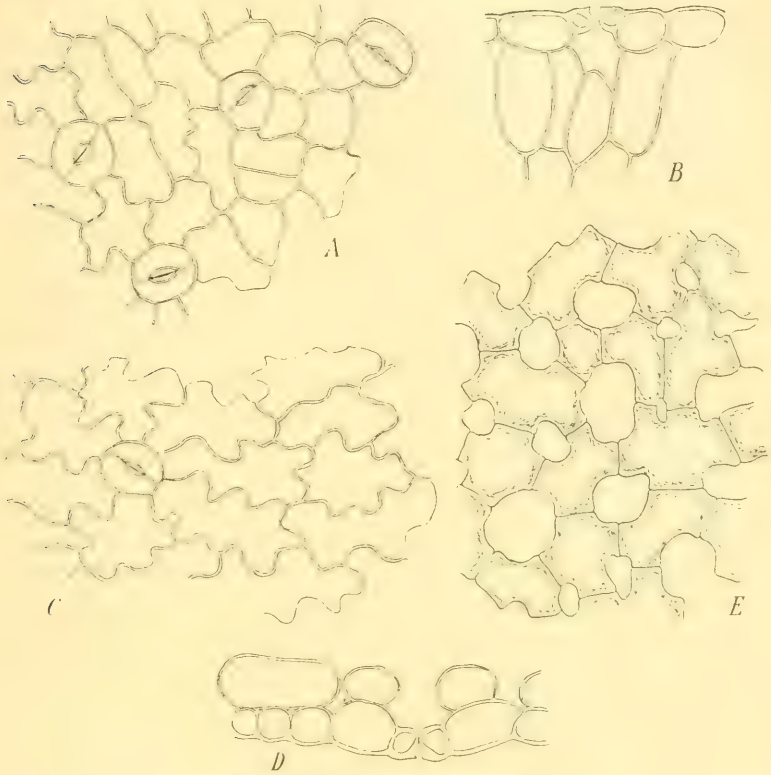

Fig. 6. *Saxifraga nivalis.*

A, Epidermis of the upper surface of the leaf. *B*, The same (transverse section). *C*, Epidermis of the lower surface of the leaf. *D*, The same. *E*, Spongy parenchyma. (*A*, *B*, *C*, *D* and *E*, $^{282}/_{1}$).

outer walls. Cuticle very slightly developed. Stomata numerous, and prominent (Fig. 6, *A*, *B*).

The epidermis of the lower surface is almost similar to that of the upper; but the cells are a little larger, and the lateral walls are somewhat more undulating. The stomata are precisely similar to those of the upper surface (Fig. 6, *C*, *D*).

Dr. Borgesen states that the stomata are equally abundant on both sides (l. c., p. 225); he has however counted 17 upon the upper surface, and 20 upon the lower per unit of surface (l. c., p. 226).

The mesophyll is fairly distinctly differentiated into a palisade-layer and spongy parenchyma; in the specimens examined by me there are three distinct palisade-layers (Borgesen found 2—3). The presence of these three layers, which implies that the specimens examined had been growing in comparatively ligh localities, harmonizes excellently with Norman's above-mentioned statement that the species occurs three times more commonly on the sunny side than on the shady side (I have not seen "shade-specimens," but Borgesen has evidently found them).

The spongy parenchyma is loosely arranged and consists of stellate cells (Fig. 6). The veins are accompanied by colourless, long-celled, usually one-layered bundle-sheaths.

The hydathodes have convex epithema and are quite similar in structure to those of *S. cernua*; they do not secrete lime.

Borgesen found scattered glandular hairs; these consist of a single row of cells, terminating in an undivided, obovate, one-celled head. Holm (l. c. Pl. X, Fig. 9) has figured a glandular hair with a two-celled head, — a feature which I have not met with. The hairs are more abundant upon the lower, and few in number upon the upper, surface.

The structure of the leaves is essentially the same in specimens from all the localities from which material has been examined; thus, I have more closely investigated specimens from Upernivik (July 10, 1887), Hold with Hope (July 10, 1891), Julianehaab (June 14, 1887), Dyrefjord (June 10, 1895), and Tromsø (June 28). The only deviation from the description given above was observed in the specimens from Hold with Hope and Dyrefjord, all of which contained a considerable quantity of oxalate of lime as crystal-aggregates in the cells of the spongy

parenchyma near to the bundle-sheaths of the veins at the base of the leaf.

As may thus be seen, the structure of the leaf is distinctly mesophytic or perhaps even hygrophytic; the prominent stomata upon both leaf-surfaces, the thin-walled epidermis, and the loose structure of the spongy parenchyma show this. The agreement between the structure of the leaf and the character of the habitat, as it has been described to me by M. Porsild, is unmistakable.

Saxifraga hieraciifolia W. K. (Figs. 7 and 8).

Saxifraga hieraciifolia W. K. occurs in precisely the same localities as *S. nivalis* (according to verbal information from M. Porsild), and it should be expected to have a structure similar to that of the latter; that it has it will be more clearly proved by what follows.

The leaf is long-stalked, oval, with distant teeth and a hydathode at the apex of each tooth (Fig. 7). The thickness is slight, less than in *S. nivalis*.

The cells of the epidermis of the upper surface (Fig. 8 *A* and *C*) have undulating walls, and rounded, wavy contours; all the walls are thin, with cuticle very slightly developed. The stomata are numerous, and prominent. Scattered glandular hairs occur which consist of a single row of cells with a one-celled head.

The epidermis of the lower surface (Fig. 8 *B* and *D*) is essentially like that of the upper; but the undulating outline of the lateral walls is more acutely angled. Stomata are numerous, and prominent. Borgesen writes that there are as many upon the upper as upon the lower surface, but yet, at the same time, records seven upon the upper and twelve upon the lower surface per unit of surface.

The mesophyll (Fig. 7 *B*, *C* and *D*) is distinctly differentiated into palisade-tissue and spongy parenchyma. Borgesen found 2—3 layers; my specimens showed two; nowhere in the leaf are they placed obliquely. The cells of the spongy parenchyma

are stellate, the whole of the tissue is highly lacunose. The veins are without mechanical tissue, but are accompanied by colourless, long-celled bundle-sheaths. The hydathodes are precisely similar in structure to those of *S. nivalis*, exactly marginal, with convex epithema; they secrete no lime (Fig. 7 *C*).

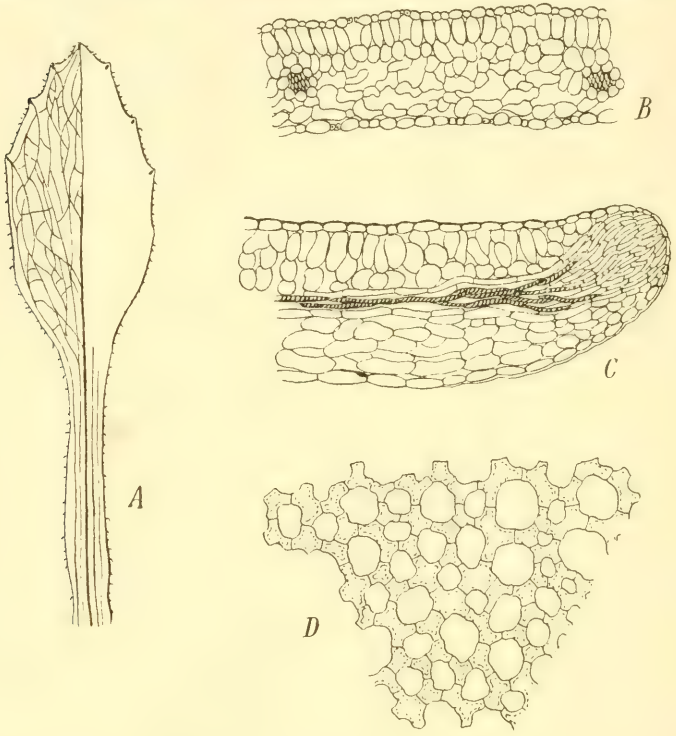

Fig. 7. *Saxifraga hieraciifolia.*
A (3/2), Leaf-form. *B*, Transverse section of leaf. *C*, The same in longitudinal section (with hydathode). *D*, Spongy parenchyma. (*B*, *C*, and *D* 50/1).

In its choice of localities this species probably nearly agrees with *S. nivalis*. In its structure (as may be seen from the above) it is more typically mesophytic than that species, the whole of its mesophyll being even more loosely arranged. Its means of protection against excessive transpiration are as slightly developed as those in *S. nivalis*; it can be distinctly seen that the palisade-tissue is less developed than in *S. nivalis*, —

from which it may perhaps be concluded that this species does not grow in quite as light localities as does *S. nivalis*.

Only specimens from Nova Zembla and Cape Tscheljuskin have been at my disposal; they were precisely similar in structure.

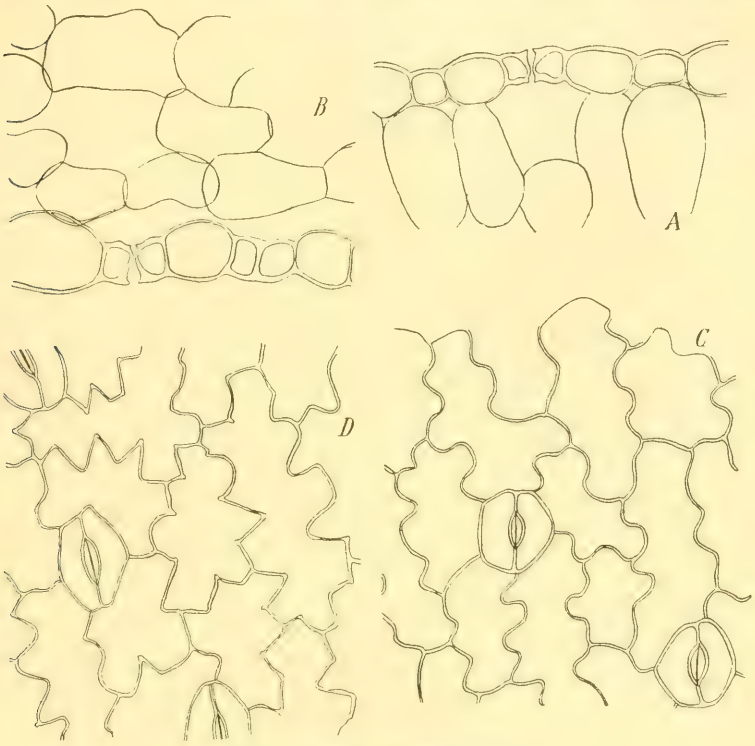

Fig. 8. *Saxifraga hieraciifolia*.
A, Upper epidermis. *B*, Lower epidermis. *C*, Upper surface. *D*, Lower surface ($^{282}/_{1}$).

Saxifraga stellaris L.

Saxifraga stellaris L. (Figs. 9 and 10) grows generally at very considerable heights on damp and cold ground, among moss, in clefts of rocks, along streams, in short it is a moisture-loving plant, as is also distinctly indicated by the anatomy of the leaf.

The leaf has slight and distant teeth and a hydathode at the apex of each tooth (Fig. 9). The epidermis of the upper surface

Fig. 10 *A* and *B*) has undulating walls which are thin everywhere. The outer walls are also thin, and have a distinct cuticle. Stomata are numerous, uniformly distributed, and prominent.

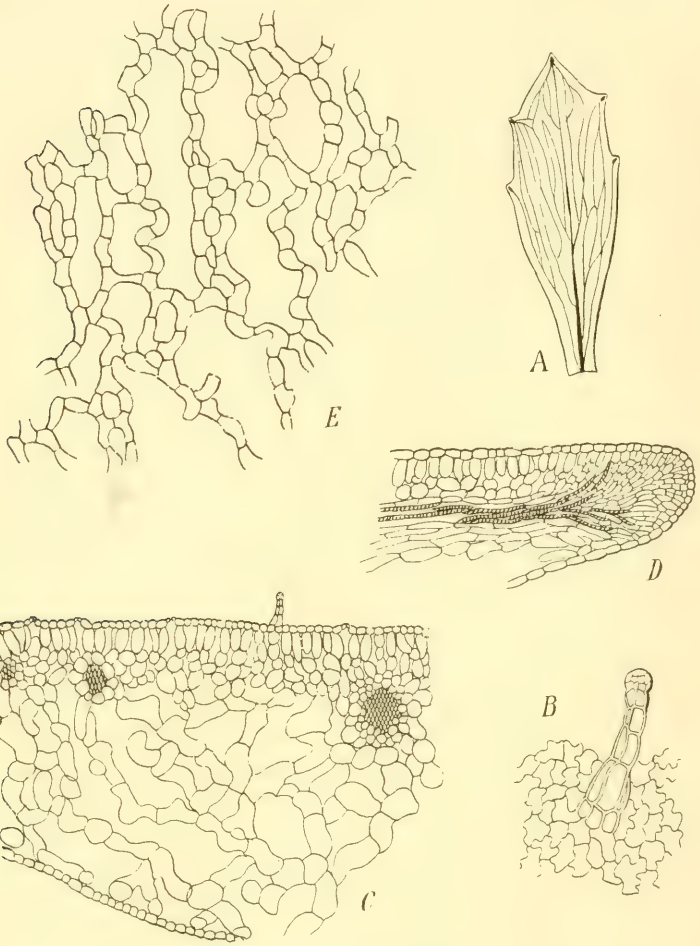

Fig. 9. *Saxifraga stellaris.*

A (2/1), Leaf-form. *B*, Epidermis of the upper surface of the leaf. *C*, Transverse section of leaf. *D*, Longitudinal section of leaf. *E*, Spongy parenchyma. (*B*, *C*, *D* and *E* 50/1).

Glandular hairs occur scattered over the whole leaf-blade; a definite head is wanting to some of the marginal hairs (Fig. 9).

The epidermis of the lower surface (Fig. 10 *C* and *D*) closely

resembles that of the upper, but the cells are greatly elongated just above the veins and at that place stomata are wanting. The stomata are placed both upon the upper and lower surface, with their apertures principally in the direction of the length of the leaf. Glandular hairs are absent.

The mesophyll (Fig. 9) is very loosely arranged. All the cells above the veins are cylindrical — either shorter or longer — with

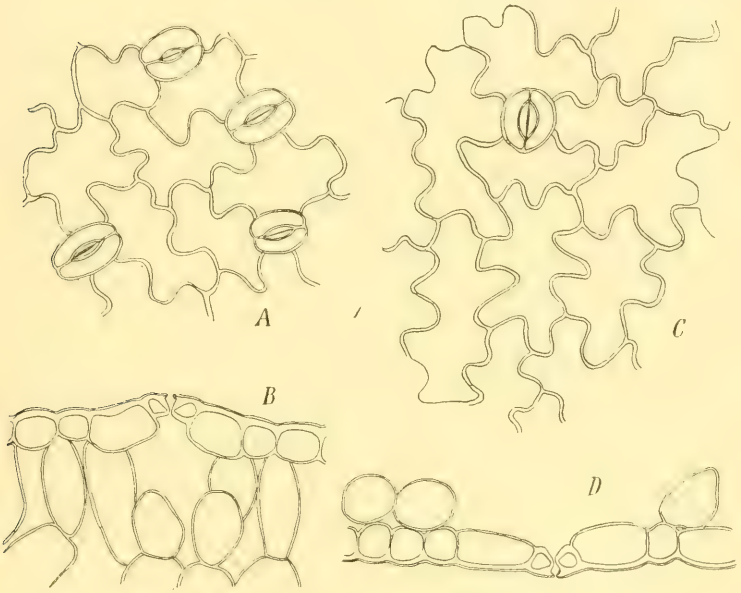

Fig. 10. *Saxifraga stellaris.*
A, Epidermis of the upper surface of the leaf. *B*, The same (transverse section). *C*, Epidermis of the lower surface of the leaf. *D*, The same (transverse section). (*A*, *B*, *C* and *D* $^{2}{}^{2}/_{1}$).

their axes at right angles to the epidermis. They can be readily distinguished from the stellate cells of the spongy parenchyma which form a very large-celled lacunose tissue. How many of the 3—4 layers of cylindrical cells are to be called palisade-cells ("collecting-cells" of Haberlandt) is quite arbitrary.

The veins are accompanied by colourless, one-layered (rarely many-layered) bundle-sheaths. Mechanical tissue is entirely

absent. The structure of the hydathode is exactly similar to that, for instance, of *S. nivalis*; it does not secrete lime.

The leaf is consequently very distinctly mesophytic (more particularly hygrophytic), and is presumably the most hygrophilous of the three species of the section *Boraphila* here dealt with, a fact which agrees excellently with its usually very damp habitat; Lazniewski also states that it is: "nicht selten im Wasser wurzelnd angetroffen" (l. c., p. 246).

Of this species I have examined specimens from Upernivik (July 18, 1886), Frederikshaab (Aug. 17, 1886), East Greenland (Sept. 4, 1885), Nova Zembla, the Færöe (July 1895), Härjedalen (Aug. 1884), Tromsø (July 21, 1885), — therefore, from widely separated localities; but they all agreed in regard to their structure.

With regard to the fleshy leaves of the bulbils, see Holm, l. c. Pl. X, Fig. 6.

3. *Dactyloides.*

The two species of this group which have been investigated agree precisely in (1) the form of the leaves (stalked and palmately lobed to palmately cleft), (2) the undulating walls of the epidermis, (3) the distinct differentiation of palisade-tissue and spongy parenchyma, and (4) hydathode with convex epithema, opening upon the upper surface of the leaf slightly within the margin. — The layers of the spongy parenchyma, from the epidermis of the lower surface to beneath the palisade-cells, differ in compactness; immediately within the epidermis the cells are polygonal, without intercellular spaces; higher up, intercellular spaces occur in considerable numbers. The difference between the two species is most apparent in the extent to which they are hairy.

Saxifraga hypnoides L. (Figs. 11 and 12).

Saxifraga hypnoides L. greatly resembles *S. groenlandica* (see below) in its anatomy.

The epidermis of the upper surface (Fig. 11 *B* and *C*) consists of two kinds of cells, (1) large, somewhat straight-walled and elongated cells, (2) irregularly-shaped cells with undulating walls. The inner, lateral and outer walls are thin (the last about 2μ in thickness). In the leaf-stalk the cells are greatly elongated, narrow

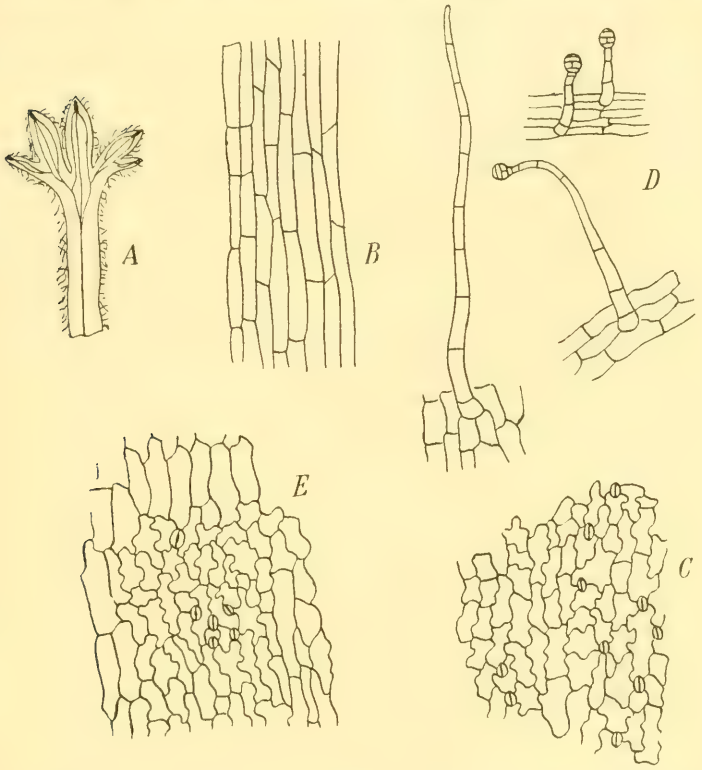

Fig. 11. *Saxifraga hypnoides.*
A (2/1), Leaf-form. B, Epidermis of the upper side of the leaf-stalk. *C*, Epidermis of the upper surface of the leaf. D, Hairs (see text). *E*, Epidermis of the lower surface of the leaf. (*B*, *C*, *D* and *E* 50/1).

and straight-walled. The stomata are placed on a level with the leaf-surface and are distributed in groups of very variable size; their apertures principally lie parallel with the longitudinal axis of the leaf. All the epidermal cells between and in immediate proximity to a group of stomata are smaller than the ordinary

epidermal cells, and their walls are far more undulating. The groups of stomata are continued as a long and very narrow stripe along — and slightly within — both the margins of the leaf-stalk, and are here also accompanied by the highly charac-

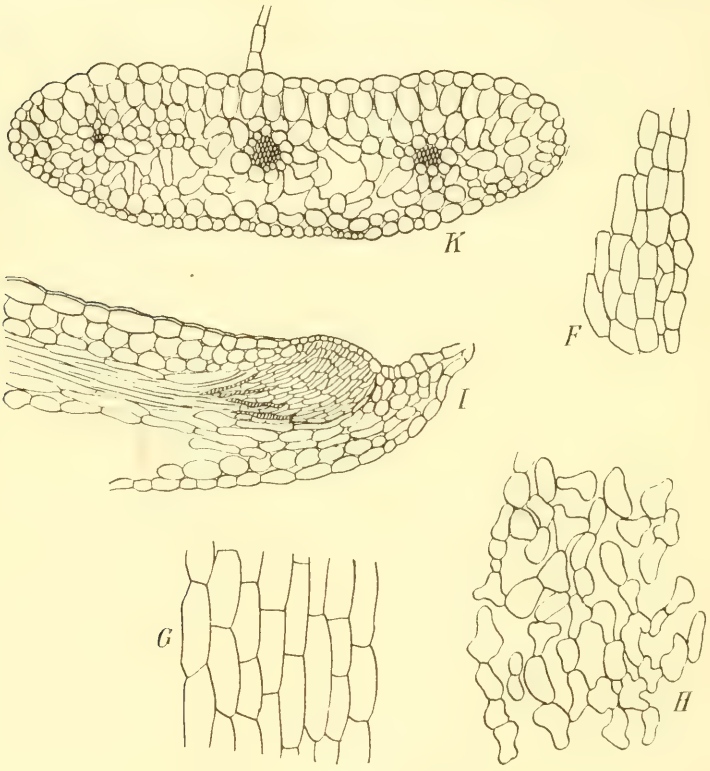

Fig. 12. *Saxifraga hypnoides.*
F, Spongy parenchyma from just below the epidermis of the leaf-blade. *G*, The same from just below the epidermis of the leaf-stalk. *H*, The same from midway between the epidermis and veins. *I*, Longitudinal section of leaf. *K*, Transverse section of leaf. (*F*, *G*, *H*, *I* and *K* $^{50}/_{1}$).

teristic small epidermal cells with undulating walls. Almost all the hairs are without apical glands; they occur invariably in the spaces between the groups of stomata and arise from the straight-walled cells — never from those with undulating walls.

The structure of the epidermis of the lower surface (Fig. 11 *E*)

is like that of the upper, only the hairs of the former are glandular (upon the leaf-stalk, however, non-glandular hairs occur).

Along the margin of the leaf-stalk there are numerous hairs similar to those upon the upper surface of the leaf.

The mesophyll (Fig. 12) is differentiated to about the same degree as in *S. groenlandica*: the palisade-cells are short (in the specimens investigated very indistinctly, or not at all, obliquely placed) and the layer passes fairly gradually into the spongy parenchyma. The latter is loose and lacunose in the middle of the leaf, but immediately within the lower epidermis it becomes very compact and polygonal, and is almost without intercellular spaces.

The veins are without mechanical tissue, and are accompanied by a bundle-sheath of elongated cells one-layered on the whole.

The hydathode is well-developed, with convex epithema, and it opens upon the upper side of the leaf-margin and does not secrete lime (Fig. 12 *I*).

The description here given is based upon the investigation of specimens gathered by F. Borgesen at Velbestad (the Færoes), July 5, 1895; that is the only material I have had at my disposal.

Saxifraga groenlandica L. (Figs. 13, 14 and 15).

Saxifraga groenlandica L. is common everywhere on the heather moors and upon the rocky flats of Greenland, and ascends to the mountain heights there and also in Norway (Warming, Norman). Grows almost as commonly on the sunny side as on the shady side upon the mountains: and usually in dry localities.

The leaves are deeply palmately cleft, the leaf-stalk is broad and flat. A hydathode occurs at the apex of each segment. Glandular hairs occur fairly numerously upon both surfaces.

The epidermis of the upper surface (Figs. 13 *B* and 15 *A* and *B*) has everywhere thin-walled cells; the latter, upon the leaf-

segments, are short and have undulating walls (straight-walled, however, above the veins and at the base of each hair). Upon the rest of the leaf-blade the epidermal cells are large and straight-walled; this also applies to the leaf-stalk, only its

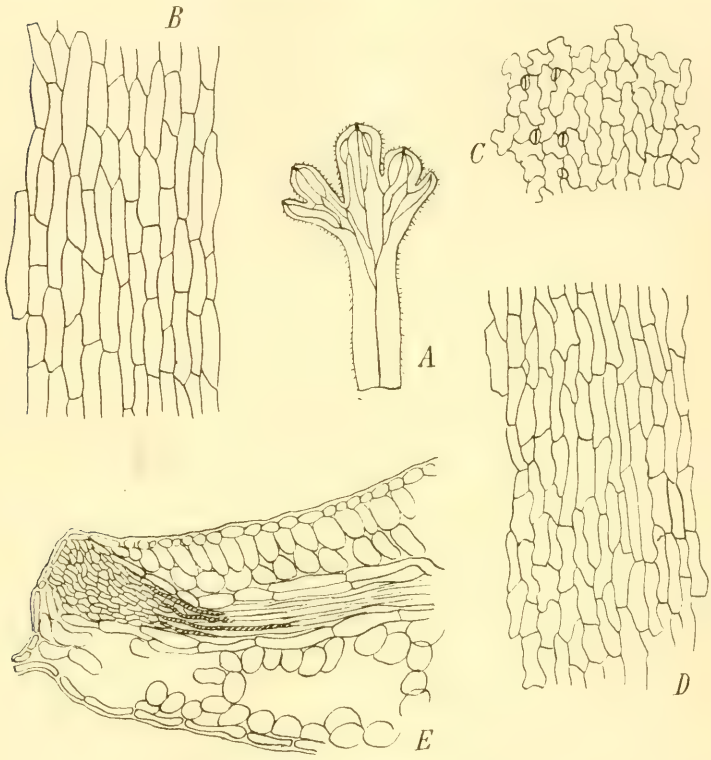

Fig. 13. *Saxifraga groenlandica.*
A (2/1), Leaf-form. *B*, Epidermis of the upper side of the leaf-stalk. *C*, Epidermis of the lower surface of the leaf, near the midrib. *D*, Epidermis of the lower surface, just above the midrib. *E*, Longitudinal section of leaf. (*A*, *B*, *C*, *D* and *E* 50/1).

epidermal cells, above the veins, are somewhat narrower than those upon the leaf-blade. Glandular hairs are found in numbers upon the leaf-segments, and are fewer in number upon the rest of the leaf-blade and along the margin of the leaf-stalk. The upper side of the leaf-stalk is very slightly hairy. The stomata are numerous and evenly distributed upon the leaf-segments;

upon the rest of the leaf-blade they are arranged in groups or rows and are always accompanied by short cells with undulating walls. Stomata are also found (very sparsely) along the margins of the leaf-stalk, accompanied by cells with undulating walls.

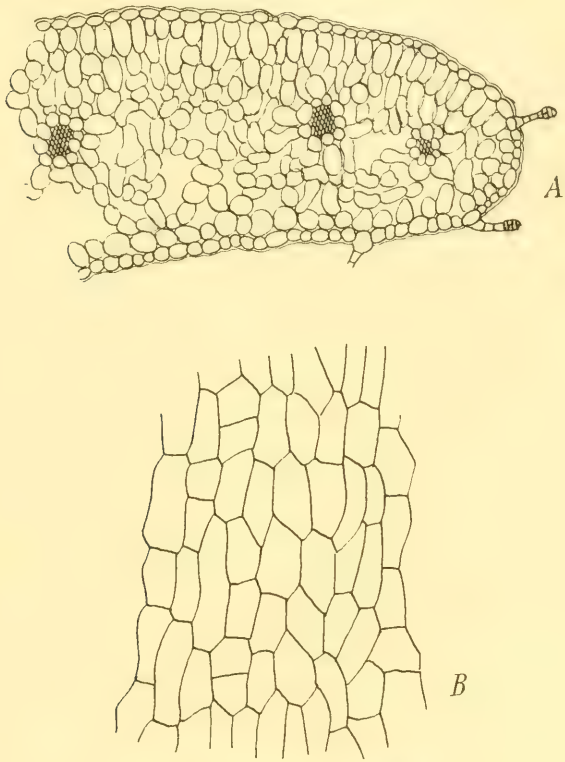

Fig. 14. *Saxifraga groenlandica.*
A, Transverse section of leaf. *B*, Spongy parenchyma from just below the epidermis ($^{50}/_{1}$).

All the stomata have their apertures parallel with the longitudinal axis of the leaf.

The epidermis of the lower surface (Fig. 13 *C* and *D*; Fig. 15 *C*) closely resembles that of the upper, only that the stomata, and the cells with undulating walls connected with them, are less numerous; the large-celled groups of hair-producing cells are more numerous than upon the upper side. Only glandular hairs occur.

The mesophyll is distinctly, but not markedly differentiated. The palisade-cells are oblique and short. The spongy parenchyma is fairly compact; (the section figured had been partly torn during preparation and has therefore been drawn as more lacunose than it was in reality). The cells of the spongy parenchyma are roundly-polygonal, unbranched or very shortly branched. The lowest layer of cells immediately within the epidermis is very compact, without intercellular spaces; the other layers (e. g. midway between the veins and the epidermis of the lower surface) are much looser in texture (Fig. 14).

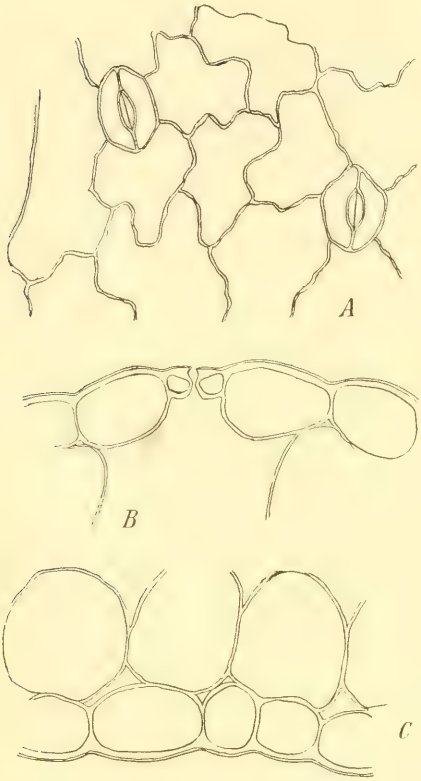

Fig. 15. *Saxifraga cæspitosa.*
Epidermis of the leaf. *A*, Upper surface. *B*, The same (transverse section). *C*, Lower surface. (*A*, *B*, *C* $^{282}/_{1}$).

The veins — like those in all the previous species — are without mechanical tissue and are surrounded by bundle-sheaths containing tannin. The hydathodes almost exactly resemble in structure those of *S. hypnoides*; they do not secrete lime.

The description here given refers to the specimens from Jan Mayen (July 22, 1896). Somewhat different from these (but otherwise resembling each other) were the specimens from Danmarks Ø (Aug. 6, 1892) and Disco (July 20, 1884), these

latter having fewer stomata upon the upper surface and none at all upon the lower surface.[1]

4. *Trachyphyllum.*

The three species which have been examined, agree in (1) the structure of the hydathode (it opens upon the upper surface of the leaf, with flattened or highly convex epithema; hydathode-cavity absent), (2) the structure of the hairs (they are everywhere irregularly-multicellular and retain this feature, either they have, or are without, an apical gland, — in contradistinction to the sections *Boraphila, Nephrophyllum, Dactyloides*), and (3) the cells of the spongy parenchyma are very little or not at all branched. — The three species differ most in the form of their leaves, but are separated also by other, smaller differences.

The chief structural features useful in diagnosis are the following: —

Leaves: —

toothed at the apex, with three acute teeth: *S. tricuspidata.*

entire: —

margin hairy along the lower half of the leaf: *S. aizoides,*

margin hairy along its whole extent: *S. flagellaris.*

Hairs: —

irregularly-multicellular marginal hairs: *S. aizoides,*

glandular hairs with irregularly-multicellular stalks: *S. flagellaris,*

(1) with globular head: *S. flagellaris,*

(2) with club-shaped head: *S. tricuspidata.*

[1] Besides the principal form I also examined specimens of the variety *palmata* from Thingvellir in Iceland (June 13, 1895). The latter is very remarkable by reason of its agreeing in almost all points with *S. hypnoides* in regard to leaf-anatomy; the only difference being that a few of the marginal hairs of the leaf are glandular.

The other differences are not characteristic enough to be given as a key; they are best seen in the figures.

Saxifraga aizoides L. (Figs. 16, 17 and 18).

Saxifraga aizoides L. according to NORMAN is a decided mountain-plant which grows both upon very wet and very dry ground, and occurs most commonly on the sunny side.

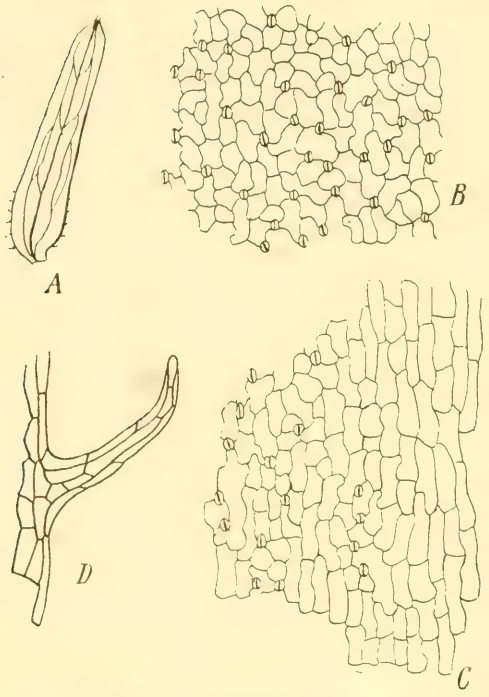

Fig. 16. *Saxifraga aizoides.*
The leaf: *A* (2/1), Leaf-form. *B*, Upper epidermis. *C*, Lower epidermis: the middle line of the leaf is to the right. *D*, Marginal hair. (*B*, *C*, *D* 50/1).

The leaf is linear, thick and succulent and terminates in a point at the base of which is found the only hydathode of the leaf. A few hairs occur along the margin towards the base; the leaf is otherwise glabrous.

The epidermis of the upper surface (Figs. 16 *B*; 18 *A* and *C*) consists of cells with slightly undulating, lateral walls and well-developed outer walls with distinct cuticle. At the base of the leaf, the lateral walls of the cells are straight and the cells are long and narrow. Stomata are absent at the base of the leaf upon its middle part, but in other places are evenly distributed. The stomata are parallel with the longitudinal axis of the leaf; they are placed on a level with the leaf-surface.

The epidermis of the lower surface (Fig. 16 *C*; Fig. 18 *B* and *D*), along the margin of the leaf, is almost exactly like that of the upper; the stomata are absent from a broad band along the middle, where the cells are elongated and narrow.

The differentiation of the mesophyll is fairly distinct. The palisade-cells, towards the apex of the leaf, are obliquely placed.

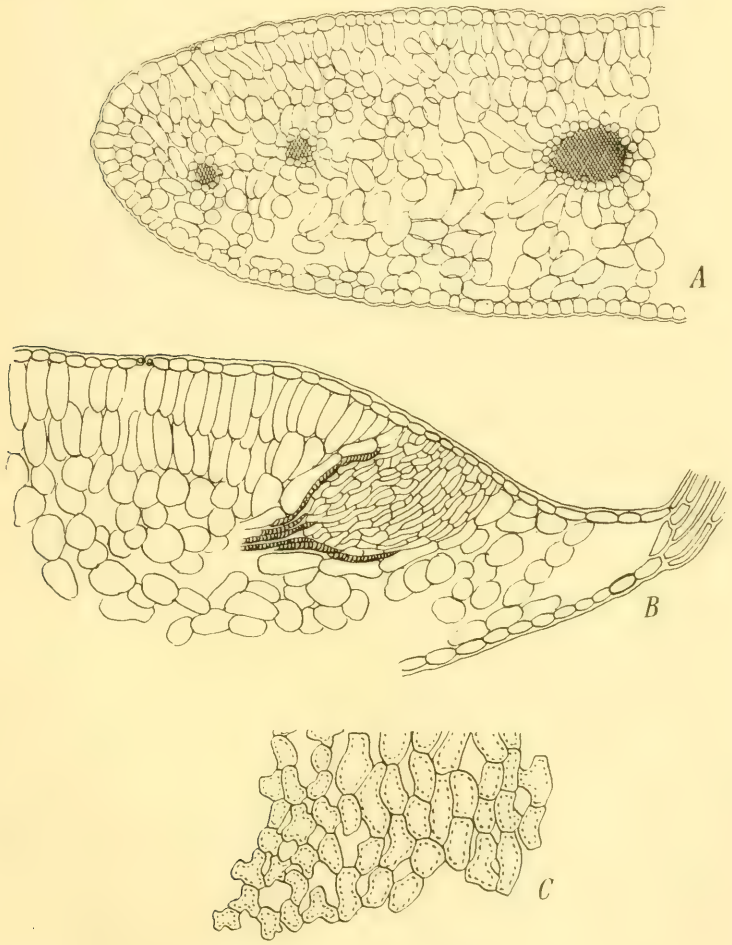

Fig. 17. *Saxifraga aizoides.*
The leaf: *A*, Transverse section. *B*, Longitudinal section. *C*, Spongy parenchyma. (*A*, *B*, *C* $^{50}/_{1}$).

The spongy parenchyma consists of roundish, shortly branched cells, which are placed more closely together, are elongated and are even more shortly branched in the middle band which is devoid of stomata.

The hydathode is situated at the apex of the leaf upon the upper surface; it does not secrete lime. The nerves are without stereom and are surrounded by a hyaline bundle-sheath.

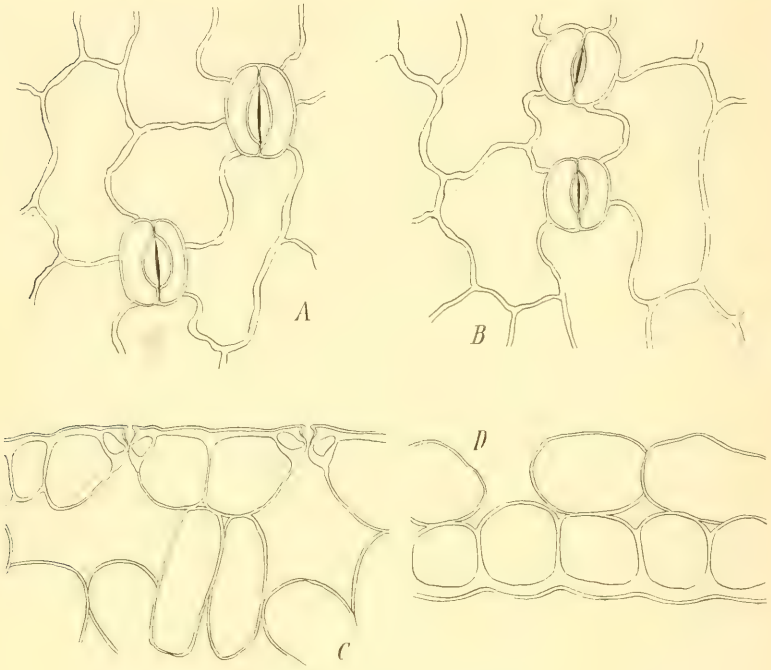

Fig. 18. *Saxifraga aizoides.*
The leaf: *A*, Upper epidermis. *B*, Lower epidermis. *C*, Upper surface. *D*, Lower surface. (*A*, *B*, *C*, *D* $^{282}/_{1}$).

I have investigated specimens from Greenland (Ilua; Ivigtut, Aug. 20, 1883) and Tromsø (1885); from all three localities the specimens were similar in all respects.

As already mentioned the plant lives both in very wet and very dry localities. The specimens examined by me were not accompanied by notes containing further information regarding

their habitats. The fact of their occurring more commonly upon the sunny side appears to suggest a predominant xerophytic tendency. At any rate, the anatomy shows, although not very decidedly, several xerophytic features (succulency, fairly well-developed epidermis, narrow leaves, etc.). Bonnier (Ann. des sciences nat., VII ser., T. XX) has grown the species in Alpine regions (1600 metres) and found the specimens grown there to contain several palisade-layers more than are found in the individuals from the lowlands, — probably a natural result of the more intense light upon mountains. The Arctic specimens, in that respect, resemble rather the lowland than the mountain specimens.

Saxifraga flagellaris Willd. (Figs. 19 and 20.)

Saxifraga flagellaris Willd. There are too few data regarding the habitats of this species to enable me to form an opinion concerning the extent of its adaptation.

The lamina is almost oval and passes gradually into the leaf-stalk. Large glandular hairs occur — along the margin, one upon the leaf-apex itself, and a few scattered over the upper surface (Fig. 19).

The epidermis of the upper surface (Fig. 20) consists of cells which have undulating walls; above the veins the cells are larger and more straight-walled than outside them. The outer walls of the cells are only fairly strongly developed, with distinct cuticle. The stomata are placed slightly above the level of the leaf-surface, are evenly distributed, and have their apertures parallel with the longitudinal axis of the leaf.

The epidermis of the lower surface (Fig. 19 *B*), along a very broad longitudinal band down the middle, has less undulating walls than upon the upper surface, and consists of longer cells. The outer walls are somewhat thickened (Fig. 20 *D*). Along the margin the epidermis, like that of the upper surface, has undulating walls, with only few stomata.

The cells of the mesophyll (Fig. 19) are not markedly differentiated; the palisade-cells are obliquely placed. The cells of the spongy parenchyma are roundish. The whole leaf is somewhat suc-

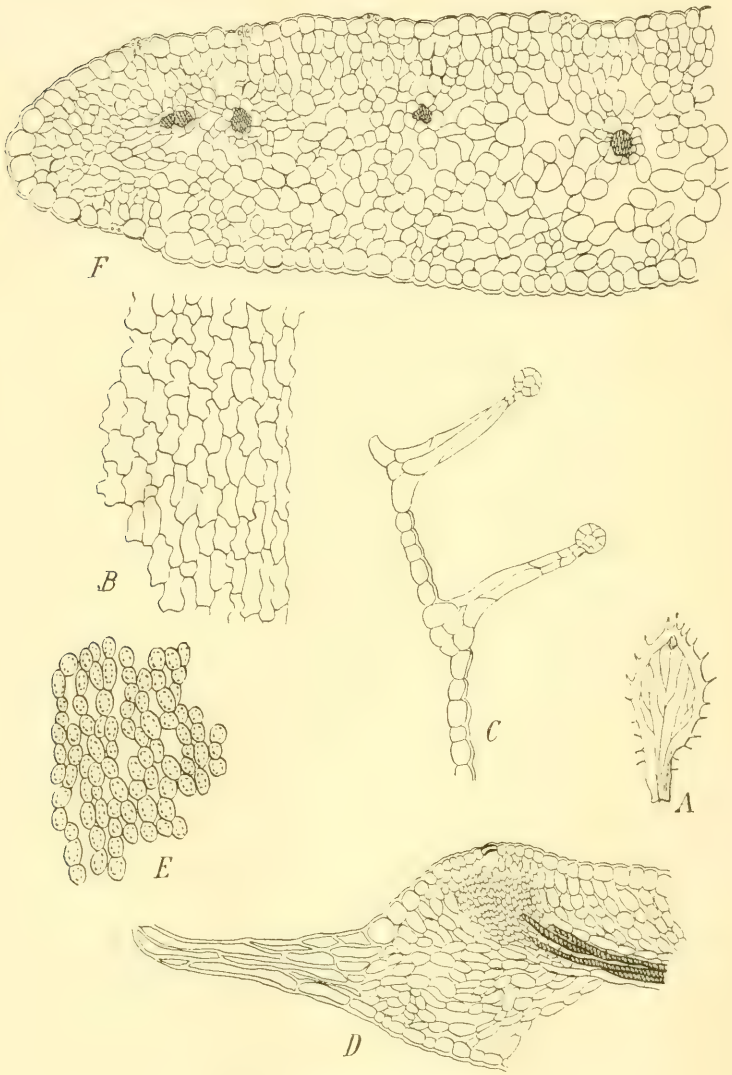

Fig. 19. *Saxifraga flagellaris.*
The leaf: *A* (2/1), Leaf-form. *B*, Lower epidermis. *C*, Marginal hairs. *D*, Longitudinal section. *E*, Spongy parenchyma. *F*, Transverse section. (*B*, *C*, *F* 56/1), (*D*, *E* 50/1).

culent, and appears, although not very decidedly so (e. g. on account of the numerous stomata upon the *upper* surface) to be somewhat xerophytic. The hydathode occurs at the apex of the leaf, upon the upper surface (Fig. 19); the epithema is

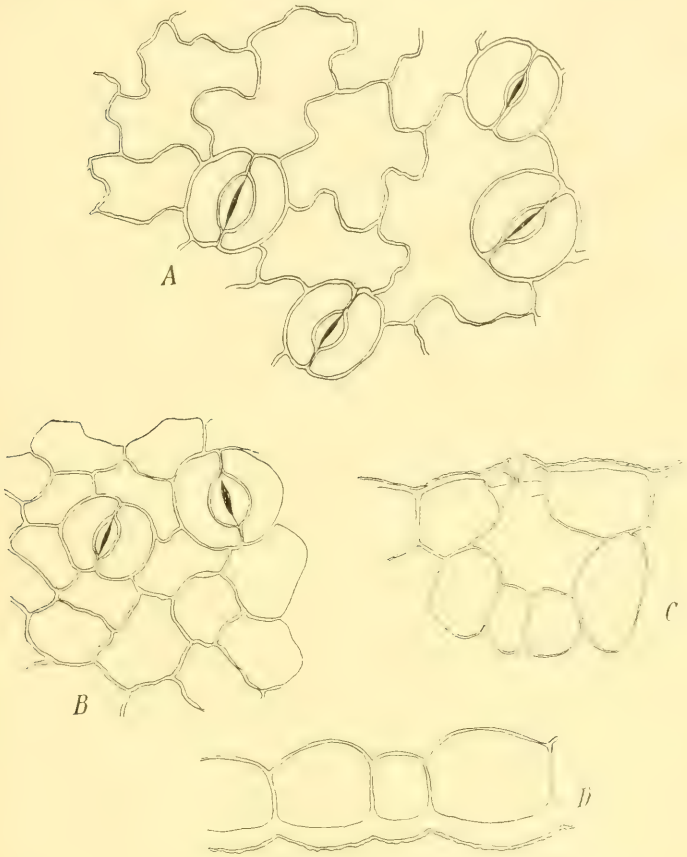

Fig. 20. *Saxifraga flagellaris.*
The epidermis of the leaf: *A*, Upper surface. *B*, The epidermis of the hydathode. *C*, Upper surface. *D*, Lower surface. ($^{280}/_{1}$).

convex. There is no secretion of lime. The veins are without stereom, and surrounded by a colourless sheath (Fig. 19).

The fleshy leaves of the bulbils contain much starch. The form of their blade is nearly like that of the foliage-leaves, but

the leaf is more short-stalked than that of the latter. The epidermis of the upper surface consists in part of very distinctly transversely elongated cells with slightly undulating lateral walls. The outer walls are 6—8 μ thick, with distinct cuticle. The stomata occur in fair numbers (not so abundantly, however, as upon the foliage-leaves), and scattered evenly over the whole surface from the apex to the base. At the apex of the leaf there is a hydathode with convex epithema. So far I could see, the stomata, both upon the leaf-blade itself and upon the epithema (the water-pores), Fig. 20, are functionless, the middle lamella in the wall common to both guard-cells not appearing to part, so that even upon the oldest leaves the stomata are permanently closed.

The epidermis of the lower surface consists of elongated cells, longer than those upon the upper surface. Outer walls 6—8 μ in thickness; cuticle present and stomata absent. Along the margin are glandular hairs, precisely similar in structure to those of the foliage-leaves.

The veins and the hydathode are exactly similar to those of the foliage-leaves, but — as already mentioned — upon the epithema the water-pores are closed.

The cells of the mesophyll are all more rounded than are those in the foliage-leaves; the cells of the layer answering to the palisade are set obliquely to the epidermis as in the foliage-leaves, although they are filled with starch-grains and are without chlorophyll; so this oblique position has absolutely no connection with any light-orientation which may have reference to assimilation. The cells of the spongy parenchyma are rounded and filled with starch.

Consequently, in these fleshy leaves are found three structural features which, for the existing functions of the leaves, appear to be useless rudiments inherited from parent-plants with foliage-leaves similar in structure to those of the present-day *S. flagellaris*.

These structural features are: —

(1) Functionless (permanently closed) stomata.

(2) Functionless hydathodes (the water-pores being closed).

(3) Light-orientated (obliquely placed) palisade-cells.

I have investigated specimens of this species from two localities, viz. Siberia (July 24, 1878, Kjellman) and Nova Zembla (Th. Holm). They were all alike.

Saxifraga tricuspidata Retz. (Figs. 21 and 22.)

Saxifraga tricuspidata Retz. a is usually found upon heaths and is xerophytic in the choice of its habitat, and this xerophytism is distinctly impressed upon the structure.

The leaf is narrow (Fig. 21 *A*), fairly thick, and, at the apex, is trifid and bears three hydathodes. The epidermis of the upper surface (Fig. 22) consists of fairly straight-walled cells, which at the base of the leaf are nearly isodiametric, but become more and more transversely elongated towards the apex of the leaf. The cells are not elongated along the midrib. Pits are present in the lateral walls. The outer walls are thick, with distinct cuticle (Fig. 22 *B*). Stomata are evenly distributed over the greater part of the leaf-blade, they are most numerous on the more exposed parts of the leaf, but are few in number at the base. They are somewhat prominent. Along the margin of the leaf are numerous irregularly-multicellular hairs. Glandular hairs occur, with long, club-shaped apical glands (Fig. 21 *B*).

The epidermis of the lower surface (Fig. 22) along the margin is, in structure, precisely similar to that of the upper surface — also in regard to its stomata. Along the middle of the leaf the cells are more elongated and the stomata few in number (more abundant, however, towards the apex of the leaf); Borgesen states that there are two per unit of surface, while the

upper side has twelve per unit. At the base of the leaf they are almost completely absent.

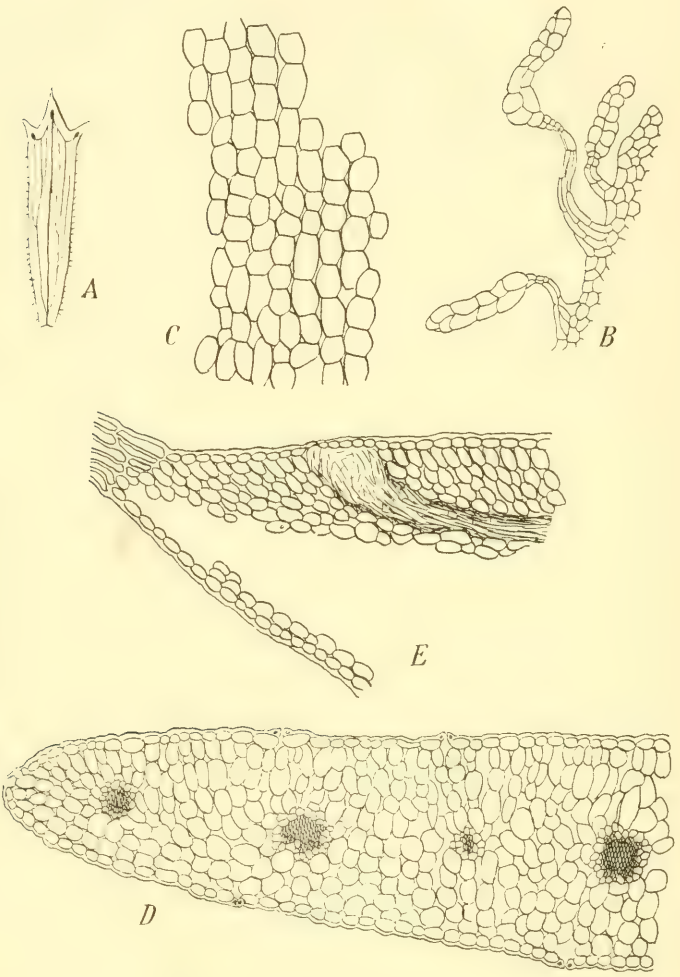

Fig. 21. *Saxifraga tricuspidata.*
The leaf: *A* (2/1), Leaf-form. *B*, Marginal hairs. *C*, Spongy parenchyma. *D*, Transverse section. *E*, Longitudinal section. (*B*, *D*, *E* 58/1), (*C* 50/1).

The mesophyll is slightly and indistinctly differentiated, and strongly recalls the condition in the section *Euaizonia* (see below). The palisade-cells are short and rounded, and

some are placed in rows which are decidedly oblique to the long axis of the leaf (Fig. 21 *D*, *E*).

The cells of the spongy parenchyma are rounded, unbranched, and most compact immediately beneath the lower epidermis (Fig. 21, *C*).

The veins are without stereom and have hyaline bundle-sheaths (Fig. 21 *D*).

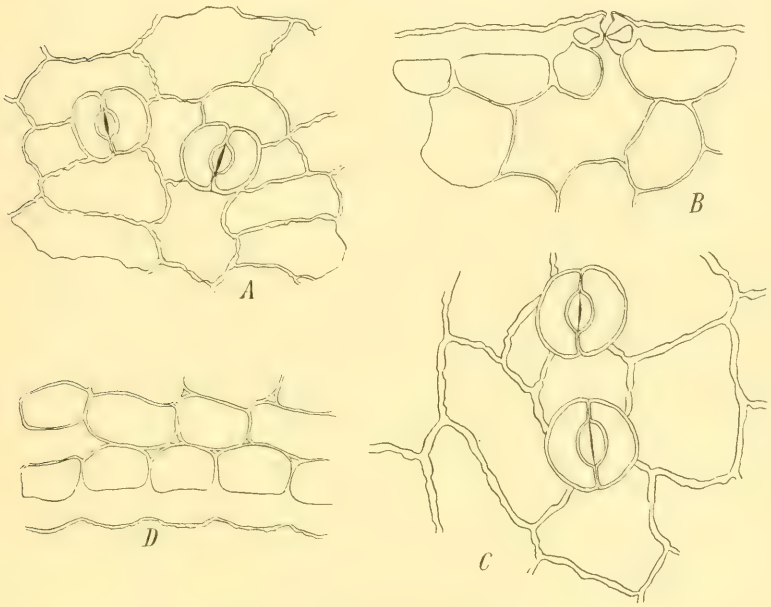

Fig. 22. *Saxifraga tricuspidata.*
The epidermis of the leaf: *A* and *B*, Upper surface. *C* and *D*, Lower surface. (*A*, *B*, *C*, *D* $^{282}/_{1}$).

The hydathode opens upon the upper side of the leaf-margin (Fig. 21); it does not secrete lime. In one solitary specimen the water-pores were gathered very closely together, six being directly in contact with each other.

I have investigated specimens of this species from Disco (July 20, 1884), Amerdlok (July 11, 1884), Upernivik (May 10, 1887). They were all alike.

5. *Euaizonia.*

The two species of this group which have been investigated show their close relationship in (1) the form of the leaves (both are spathulate, and serrate, with a hydathode at each tooth), (2) the distribution and structure of the hairs, (3) the transverse elongation of the epidermal cells of the upper surface and the longitudinal elongation of those of the lower, (4) the pits in the radial walls of the epidermal cells, (5) the structure of the palisade-tissue and of the spongy parenchyma, (6) the structure of the veins, (7) the hydathodes with a cavity, and with secretion of lime, (8) and the stomata, surrounded by 4—6 smaller cells. The differences between the two species are so slight, that on the basis of the anonymous section at hand it would be difficult, if not impossible, to separate them from each other with any certainty; presumably they differ more particularly as regards the epidermis of the upper surface of the leaf, which in *S. Aizoon* has more decidedly transversely elongated cells than in *S. Cotyledon*. As far as is known, wax is absent from the epidermis of the latter species, while it is found in *S. Aizoon*. A key to their determination would therefore be as follows: —

Epidermal cells of the upper surface
very distinctly transversely elongated: *S. Aizoon*,
somewhat indistinctly, or more rarely not at all transversely elongated: *S. Cotyledon*.

Saxifraga Cotyledon L. (Figs. 23 and 24.)

Saxifraga Cotyledon L. This species is a Sub-alpine lowland plant which here and there extends almost down to the sea-level and scarcely ever extends higher into the mountains than about 500 feet; found most commonly at elevations of 200—300 feet above the sea. It grows partly upon level, partly (and most commonly) upon sloping ground, where it is

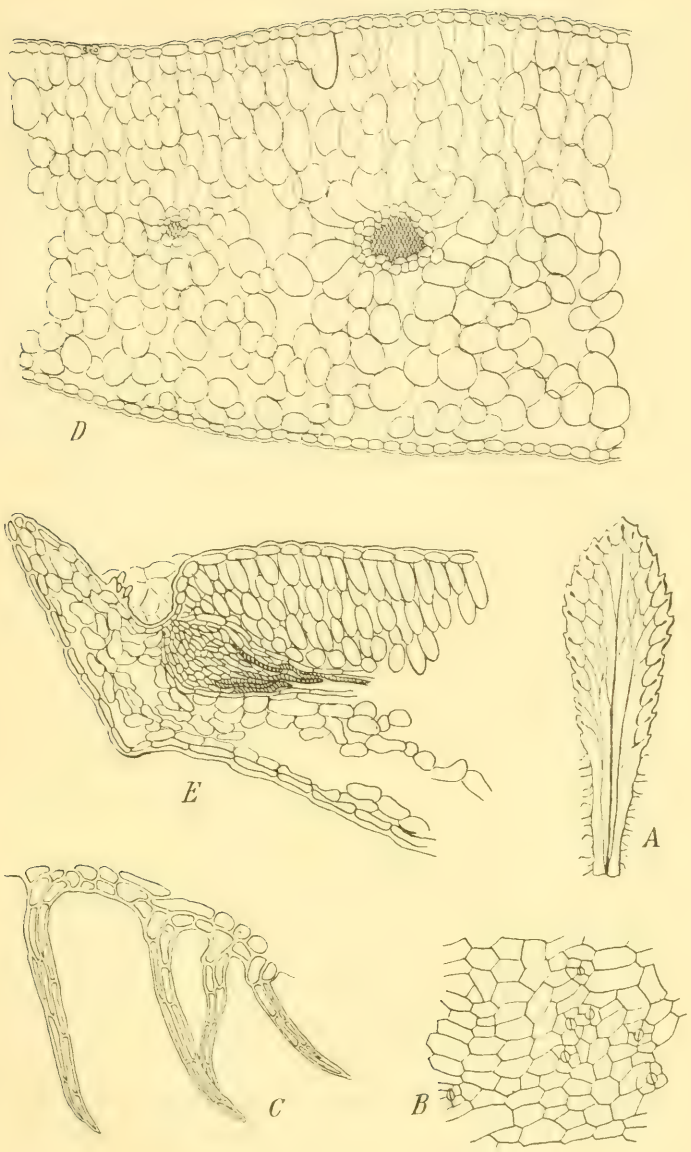

Fig. 23. *Saxifraga Cotyledon.*

The leaf: *A* (2/1), Leaf-form. *B*, Epidermis of the middle of the upper surface. *C*, Marginal hairs. *D*, Transverse section. *E*, Longitudinal section. (*B*, *C*, *D*, *E* 50/1).

about five times as common upon the southern side as upon the northern, while it scarcely ever occurs on the eastern and western sides (Norman, l. c., pp. 294—95).

The leaves are in a dense rosette, which somewhat recalls *Sempervivum*. Each of the teeth upon the leaves is provided with a hydathode (Fig. 23 *A*). The leaves are fairly thick.

The epidermis of the upper surface (Fig. 23 *B* and Fig. 24) consists of polygonal, straight-walled, usually transversely elongated cells; the lateral walls are rather thick (3—4 μ), with numerous thin-walled parts (pits). The outer wall is thick (8—10 μ), with a strong cuticle; stomata occur abundantly, but are absent towards the base, are more numerous upon the exposed parts of the leaves, and are all surrounded by 4—6 small cells; they project above the leaf-surface (Fig. 23 *B*).

The epidermis of the lower surface (Fig. 24) consists of elongated cells which are similar in structure to those upon the upper surface. The stomata are absent from along the whole of the middle band and from the base of the leaf, exactly as in *S. Aizoon* (a specimen from Kobbefjord — which see); but they are numerous along the margin, where the epidermal cells are less elongated, and are decidedly most abundant upon the lower side. Along the margin of the leaf-base there are some thick, irregularly-multicellular hairs (Fig. 23 *C*).

The mesophyll consists of remarkably homogeneous cells; the palisade-cells are somewhat longer than the cells of the spongy parenchyma, and approximately barrel-shaped (Fig. 23). They are placed, especially towards the apex, obliquely to the epidermis, and there are numerous, rather large intercellular spaces between them. Below, the palisade merges imperceptibly into the more isodiametric, unbranched cells of the spongy parenchyma, between which the intercellular spaces are still larger. The vascular bundles are without stereom, but are surrounded by a (usually one-layered) bundle-sheath which contains tannin. Sphaerocrystals, the nature of which has not been more

closely investigated, are found (in spirit-material) precipitated in some of the cells of the mesophyll which differ in no other respect from the rest of the mesophyll.

All the veins terminate in a hydathode (Fig. 23). The latter opens into a cavity upon the surface of the leaf and secretes

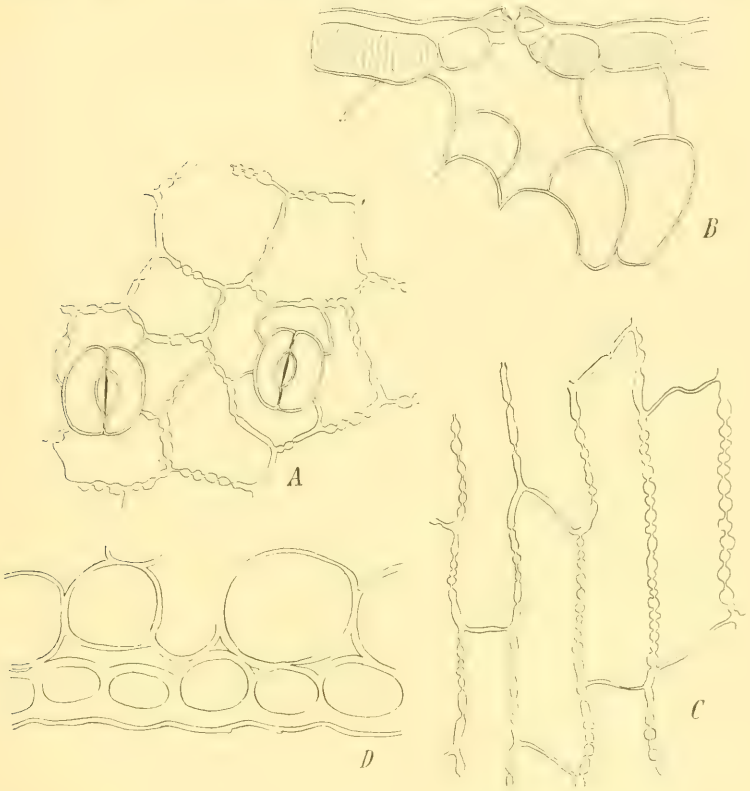

Fig. 24. *Saxifraga Cotyledon.*
The epidermis of the leaf: *A* and *B*, Upper surface. *C* and *D*, Lower surface. (*A*, *B*, *C*, *D* $^{282}/_{1}$).

lime abundantly which in many cases entirely fills the cavity and spreads outside it (this is omitted in the figure).

Bonnier has proved that different specimens of this species, collected partly in the Arctic and partly in the Alpine regions of Central Europe, can be distinguished from each other by

the former having less markedly differentiated palisade-tissue than the latter. This somewhat indistinct differentiation also found by me in the Arctic specimens of *S. Cotyledon* at my disposal agrees closely with characters found by Bonnier in Arctic specimens; the same investigator (Rev. gén. d. bot., Tome VI, p. 514) has demonstrated this feature very distinctly in *S. oppositifolia* (see below). His figure of the Arctic leaf of this latter species is good and agrees closely with the results of my investigations.

Saxifraga Aizoon Jacq. (Figs. 25, 26 and 27).

Saxifraga Aizoon Jacq. occurs upon sunny cliffs, and sometimes upon rather wet moraine, and is xerophytic. Its whole

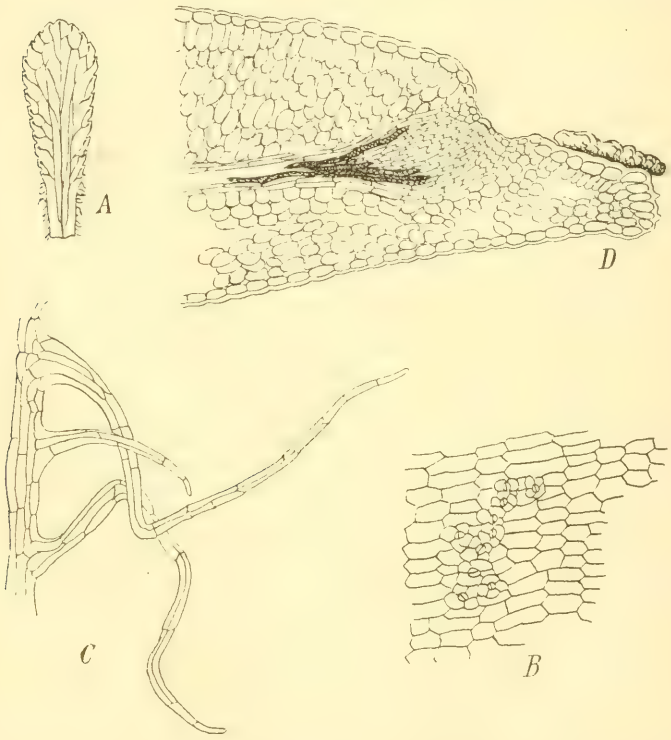

Fig. 25. *Saxifraga Aizoon.*
The leaf: *A* (2/1), Leaf-form. *B*, Epidermis of the upper surface. *C*, Marginal hairs. *D*, Longitudinal section (50/1).

morphological and anatomical structure has a great many points in common with that of *S. Cotyledon* (e. g. the succulent leaf-rosettes, the external form of the leaf, etc.).

The epidermal cells of the upper surface (Figs. 25 *B* and 27) of the leaf are elongated longitudinally at the base, but higher up in the leaf they become transversely elongated. The outer walls are thick, with distinct cuticle. The stomata are absent from the leaf-bases, they do not appear until above the

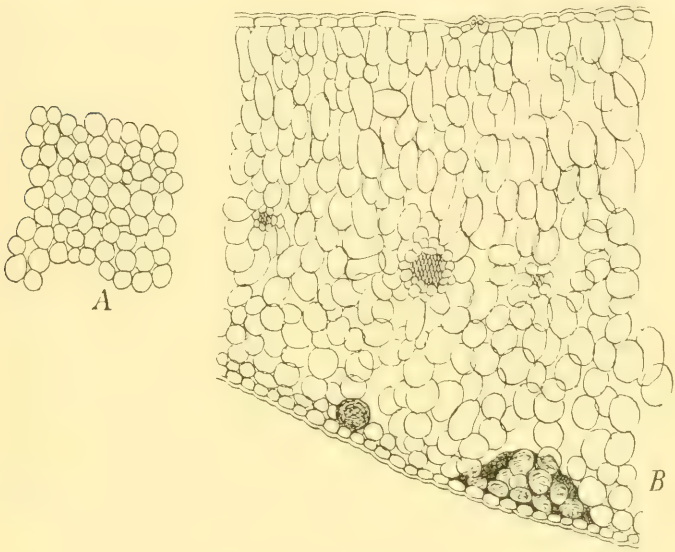

Fig. 26. *Saxifraga Aizoon.*
The leaf: *A*, Spongy parenchyma. *B*, Transverse section (below to the left, a tannin-cell, to the right a sphaerocrystal). (*A*, *B*, $^{50}/_{1}$).

marginal hairs. They are surrounded by, usually, four smaller cells (cf. Thouvenin l. c.) and are not definitely orientated (e. g. not parallel with the midrib).

The lower epidermis (Fig. 27) is of elongated cells at the base of the leaf and is continued as a median band of similar elongated cells without stomata, which gradually narrows towards the apex of the leaf. To the right and left of this band occur areas which are of smaller cells, and there all the stomata are placed in

groups. These two marginal bands commence above the marginal hairs of the leaf and widen continuously towards the apex to the sacrifice of the middle band. Therefore stomata are quite absent from the leaf-blade below the point at which the marginal hairs begin, they all occur towards the apex of the leaf.

Borgesen states (l. c., p. 225) that the stomata are more abundant upon the upper surface, but yet, at the same time, records that it has eight, while the lower surface has twelve, per unit of surface. The latter statement unquestionably corresponds better with my observations. Lazniewski's statement that the stomata are entirely absent from the exposed leaf-apices of many rosette-plants does not at all agree with the conditions found by me in this species, which has all its stomata especially placed in the most exposed parts of the leaf.

A wax-covering is present in the form of small grains of irregular form upon the apical, exposed parts of the upper side of the leaf.

The description given above of the mesophyll of *S. Cotyledon* exactly suits that of the present species. The palisade-cells are very slightly differentiated, are barrel-shaped, and the tissue merges below imperceptibly into the spongy parenchyma with its more isodiametric, unbranched cells (Fig. 26).

The palisade-cells are more or less obliquely placed towards the apex of the leaves. Lazniewski (l. c.) has found this to be the case in many rosette-plants, and connects it with the peculiar way in which light falls upon such a rosette with its obliquely erect leaves (this feature was first pointed out by Pick).

At the base of the leaf the difference between the palisade-tissue and the spongy parenchyma is even further obliterated, nor does any obliquity occur there; the whole mesophyll is homogeneous, exactly like that found by Lazniewski in many Alpine rosette-plants.

In many of the cells of the mesophyll there are quantities of tannin, which gives the usual reaction with iron. Besides these scattered tannin-idioblasts there are found, precipitated

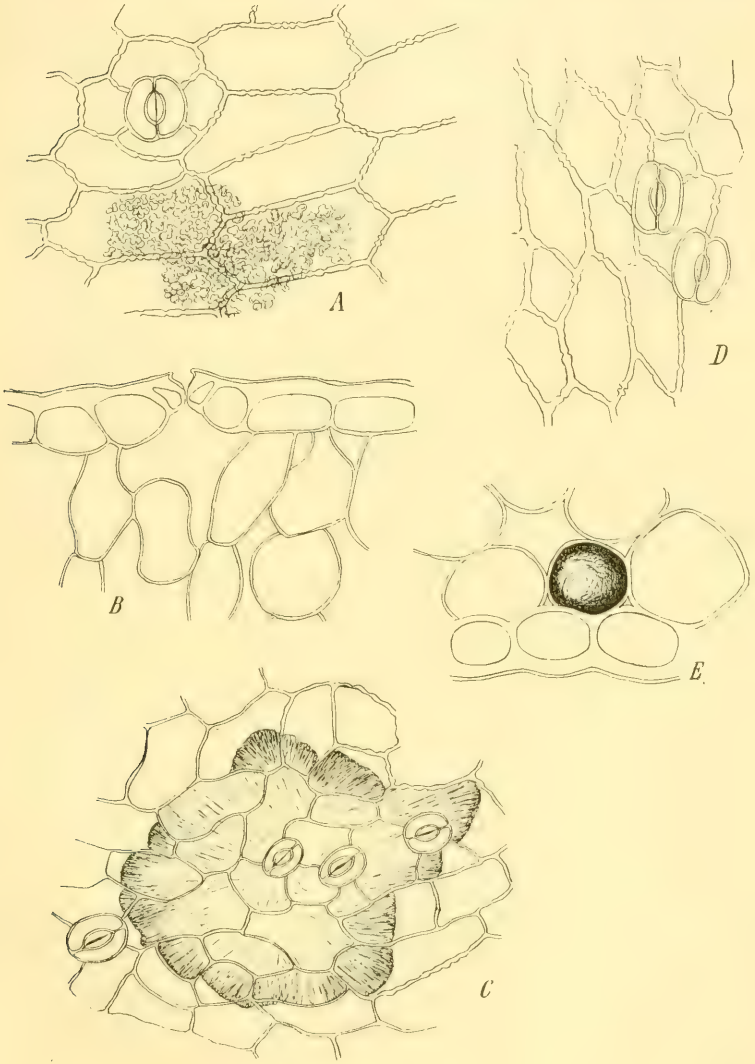

Fig. 27. *Saxifraga Aizoon.*

The epidermis of the leaf: *A* and *B*, Upper surface. *C*, Lower surface (a large sphaero-crystal is seen immediately beneath the epidermis, probably precipitated by alcohol. *D* and *E*, Lower surface (C $^{175}/_{1}$), (A, B, D, E $^{282}/_{1}$).

in many places (in spirit-material), large sphaerocrystals (the composition of which has not been more closely investigated) among the cells immediately beneath the epidermis (Fig. 27). Sphaerocrystals also occur here and there in the epidermal cells. In none of these places — as far as I could judge from living material — do these crystals occur in connection with living cells; they are probably an alcoholic precipitate.

The veins are accompanied by bundle-sheaths containing tannin (Fig. 26). Each tooth of the leaves is provided with a vein which terminates in a hydathode with a large cavity (Fig. 25). The epidermis of the hydathode has 1—2 water-pores and some of the cells are elongated as papillæ. Lime is abundantly secreted—much more abundantly than in *S. Cotyledon*.

I have investigated specimens from Kobbefjord (June 29, 1884), Holstensborg (July 17, 1884), Sarfanguak (July 15, 1884) in West Greenland, from Ryder's expedition to Scoresby Sound (July 28, 1887), and from Vatnsdal (Aug. 6) in Iceland. They were all almost identical; only the specimen from Sarfanguak had more ample lime-incrustations upon the hydathode than had the rest.

The plant grows usually in dry localities (part of my material came from sunny southern slopes); its whole character is rather decidedly xerophytic; but here also reference should be made to the occurrence of stomata upon the exposed parts of the leaf, as in *S. Cotyledon*.

Leist (1889) maintains that in Alpine districts this and the former species have a leaf-structure which more closely resembles that of shade-leaves. Lazniewski (l. c.) disputes this, and maintains that the Alpine *Saxifraga* are xerophytes. — It must be owned that Leist's assertion carries no conviction, as the necessary figures are wanting, and the descriptions are, by themselves, unsatisfactory.

6. *Porphyrion.*

Saxifraga oppositifolia L. (Figs. 28 and 29).

Saxifraga oppositifolia L. extends to the highest summits of the mountains into the snow-flora (Norman, Warming). Grows on dry, stony ground, upon the rock itself or among large boulders. Consequently it is a xerophyte, and shows this very distinctly in its internal structure. The leaf has only one hydathode at the apex. The marginal hairs are irregularly multicellular.

The upper epidermis (Fig. 29) has fairly straight lateral walls, with numerous pits. The outer walls differ in thickness in the different parts of the leaf; towards the apex they are very thick, and from thence become gradually thinner towards the leaf-base. The cuticle is distinct and very finely wrinkled. The stomata, with fair regularity, are placed parallel to the length of the leaf, only a few depart somewhat from this position. Their distribution upon the leaf-blade is very remarkable. They are entirely absent from the extreme tip of the apex, upon which is the hydathode. Immediately behind the apex they occur in a broad band across the leaf and are partially continued along the under-side of the leaf-margin.

The epidermis of the lower surface (Fig. 29) closely resembles that of the upper; its cells, however, are somewhat more elongated longitudinally. The distribution of the stomata is like that upon the upper side.

The palisade-cells of the leaves (Fig. 28), at the exposed apex, are very distinct and occur both upon the upper and lower surface, the leaf being directed sharply upwards. Further down towards the base the differentiation between palisade-tissue and spongy parenchyma disappears entirely. The spongy parenchyma consists of rounded, unbranched cells, fairly compact; within the epidermis towards the leaf-base there is a single layer of cells which is quite without intercellular spaces. As already men-

tioned, the parts of the leaf which are exposed to the light possess a spongy parenchyma developed in the form of palisade.

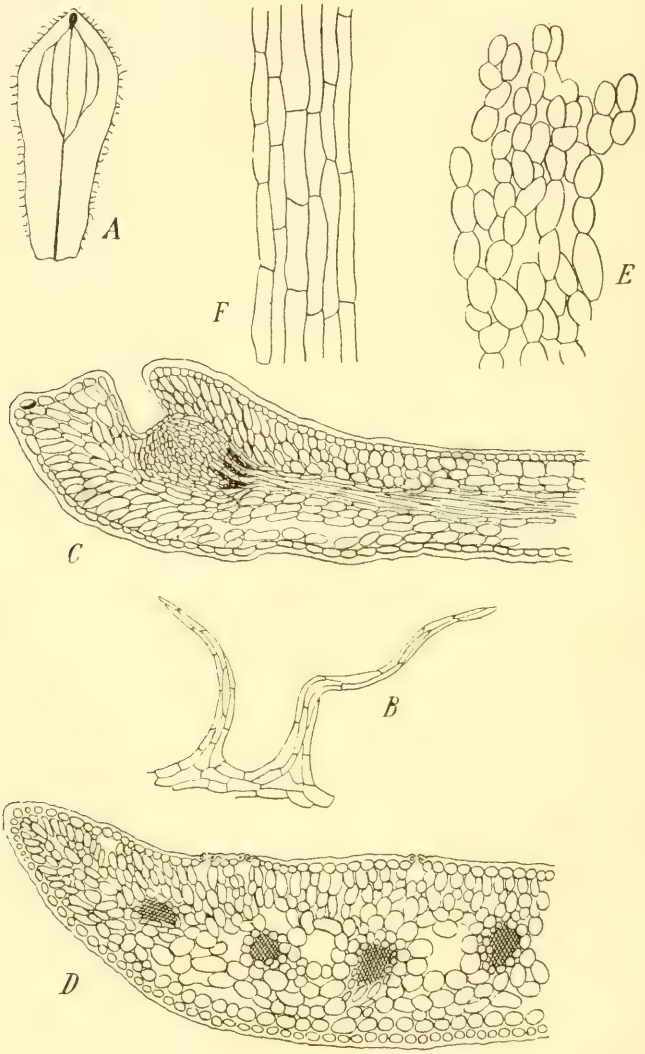

Fig. 28. *Saxifraga oppositifolia.*

The leaf: *A* (7/1), Leaf-form. *B*, Marginal hairs. *C*, Longitudinal section. *D*, Transverse section. *E*, Spongy parenchyma. *F*, Spongy parenchyma from the leaf-stalk. (*B*, *C*, *D*, *E*, *F* 50/1).

Lazniewski (Flora, 1896) has described the leaf-anatomy of this species very accurately and has given figures of it. He points out that the leaves are seated so closely together that, for the greater part, they overlap each other, and he then emphazises the fact that only that part of the leaf which is covered by neighbouring leaves bears stomata abundantly, while

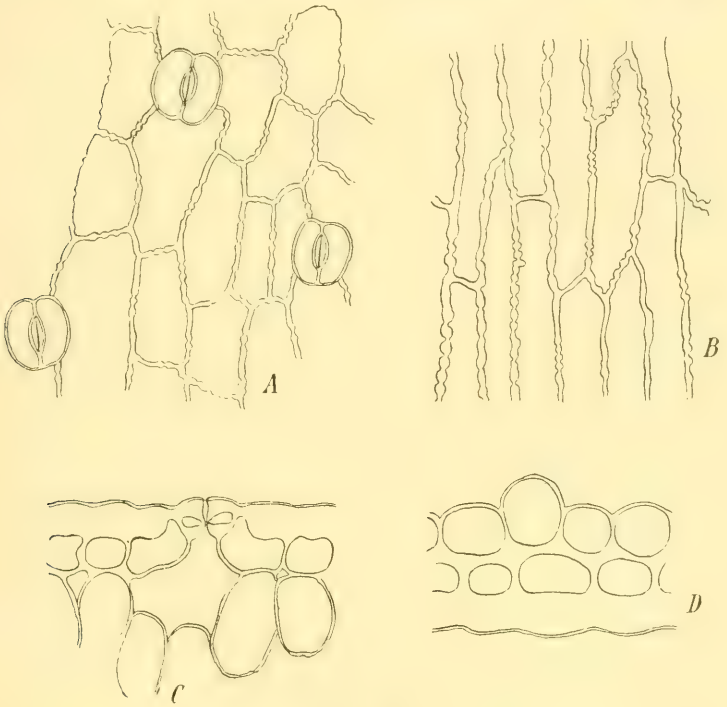

Fig. 29. *Saxifraga oppositifolia.*
The epidermis of the leaf: *A* and *C*, of the upper surface; *B* and *D*, of the lower surface. (*A*, *B*, *C*, *D* $^{282}/_{1}$).

the light-exposed leaf-apex is almost without them, and has a very thick outer epidermal-wall and true palisade-cells (which, on the other hand, are absent from the shaded part). Lazniewski maintains that this distribution of the stomata is also found in rosette-plants and regards it as a protection against excessive transpiration.

In all the specimens examined by me I found the distribution of the stomata to differ somewhat from that mentioned by Lazniewski. His Fig. 11 (l. c., p. 239) shows the stomata to be below the line *A—B*. But in all the Arctic specimens the stomata-bearing band begins still higher up and only the oblique surface upon which the hydathode is situated is devoid of them. In the fully expanded specimens that part of the leaf which bears the stomata, is not at all shielded from exposure to light, in fact, the stomata occur especially upon the strongly exposed parts of the leaf which possess palisade-cells, with the exception only of the oblique surface bearing the hydathode. Hence we must resort to quite a different explanation of the distribution of the stomata: — They are absent from the oblique surface bearing the hydathode, which is the only part of the leaf that in the bud-condition of the shoot is exposed to light and air; we have here an instance of a primitive bud-protection which comprises only the very young leaves, while already the oldest leaves of the bud, which are exposed to the elements, are somewhat expanded before winter sets in.

Besides, the stomata are absent from the base of the leaf, — where I think they might be expected to occur in large numbers if Lazniewski's hypothesis should also apply to the Arctic species. The absence of stomata from the base of the leaf is to be connected with the fact that the "leaf-base" is in reality the morphological leaf-stalk (below the common starting point of the veins), where neither palisade-cells nor stomata occur (compare *S. groenlandica* and *S. hypnoides*); consequently the other *Saxifraga*-species have no stomata upon their leaf-stalks. Lazniewski's assertion that the stomata are hidden in "interfoliar spaces free from air-currents" does not apply at all to the Arctic specimens, as (1) the stomata are situated chiefly in the parts of the leaf possessing

palisade-cells and (2) they are entirely absent from the "interfoliar-spaces" (i. e. the morphological leaf-stalks).

As regards the seasonal biology of the leaves it may be observed that at the base of the buds which live over the winter partially expanded leaves usually occur, which probably assimilate for some length of time before beginning their winter-rest; but of course this has not been proved. The buds, moreover, are sharply limited below by dead leaves, which persist upon the stems for several years. Bud-scales are absent, and the only protection the younger leaves have is due to the circumstance already mentioned, that they are without stomata exactly upon the small space containing the hydathode which, in the bud-condition, is the most visible and most exposed part of the leaf.

A specimen from East Greenland (Danmarks Ø), collected February 28, 1892, was remarkable with regard to the arrangement of its chlorophyll-grains, the latter (in the two upper palisade-layers) having sunk down to the bottom of the cells, of which the upper part was occupied by a large vacuole. The other cells of the mesophyll showed no such feature. Whether this circumstance (which was not observed in any leaf gathered during the period of growth) is really a common winter-phenomenon in *S. oppositifolia* in Arctic regions, or is due to the imperfect way in which ordinary spirit-material on the whole is fixed when collected, I am not prepared to state with any certainty.

I investigated plants of *S. oppositifolia* from the following places: — Upernivik (May 17, 1887), Danmarks Ø (Febr. 18, 1892) and Julianehaab (May 22, 1887) in Greenland, Jan Mayen (July 22, 1896), Nova Zembla, Vallanæs (Iceland; Dec. 21, 1893) and from the Botanic Garden in Copenhagen (April 18, 1907). The leaves of all these species agreed very closely in all anatomical details. Any difference which could be attributed to the influence of the different geographical conditions could not be

demonstrated in spite of much investigation; the leaves all agreed with the description given.

The cultivated specimen from the Botanic Garden alone had very long internodes, but the structure of the leaf was exactly like that of, for example, the specimens from either Upernivik or Jan Mayen.

We have now seen what is the leaf-anatomy of the different species. It appears that the species belonging to any systematic section show greater anatomical relationship mutually, than they show with species of other sections. The structural features which vary least are here also of the most value as a supplement to the microscopical section-diagnosis. The structure of the hydathode and the appearance of the radial walls of the epidermis appear to be generally the characters which are least influenced by external conditions and which with a certain degree of constancy, remain uniform within the same section.

There are three different types of hydathodes: —

(1) Hydathode marginal, situated actually at the edge of the leaf; no secretion of lime: *Boraphila*, *Nephrophyllum.*

(2) Hydathode upon the upper surface of the leaf-margin; no cavity; no lime: *Dactyloides*, *Trachyphyllum.*

(3) Hydathode upon the upper surface of the leaf-margin; cavity present; lime secreted: *Euaizonia, Porphyrion.*

The other structural features, such as the thickness of the epidermis and the structure of the mesophyll, which are more easily influenced by external conditions, also are similar within each section, as may be seen from what has been written above. To this must be added, that Bonnier's investigations are greatly in favour of the idea that the structure of the mesophyll

in the species here investigated would be different if they were cultivated in Alpine regions. When nevertheless they agree within each section in Arctic regions, this proves that although the structure of the mesophyll varies according to climate, yet it varies correspondingly in the species belonging to the same section. Leist found that *S. Aizoon* and *S. Cotyledon* (from the Alps) had exactly the same structural features; I, also, in my Arctic specimens, found that these two species, belonging to the same section, had quite similar leaf-structure, — but it must be admitted it was a structure which was entirely different from that found by Leist in his Alpine specimens — a good example, therefore, of corresponding variation in closely related species.

If we wish to define how the Arctic species of *Saxifraga* are adapted in their leaf-anatomy to their natural surroundings, emphasis must be laid upon the fact that the same characteristic tests cannot be applied to all the species investigated, taken as a whole. They cannot as a matter of fact be termed either xerophytic or hygrophytic, these words having on the whole only a relative value, as they do not state anything about the plant's absolute relation to water-absorption and transpiration. If, on the other hand, we can show that the Arctic *Saxifragas* are either more, or else less, xerophytic than their Alpine colleagues, that would be a positive result of great significance, as it would bring about a comparison from which, to a certain extent, we might be justified in deciding how Alpine plants must adapt themselves in order to be able to live under the external conditions of Arctic regions, and vice versa. My endeavour has been to give as accurate a description of Arctic species as possible; future investigations must prove wherein such species differ from Alpine species. Bonnier has already attempted something of this kind, but more exhaustive investigations are highly desirable. The variations occasioned by external conditions are, in the greater number

of cases, so small that mere descriptions cannot indicate them, or can do so only with great difficulty and with little precision; detailed figures elucidate the variations better. It is my opinion, that much of the constant dispute as to how far Alpine plants are xerophytic or non-xerophytic in character is a merely verbal difference which might have been avoided if the several authors had given sufficient figures (for instance, as many as Bonnier or even more, by preference), — instead of the many verbal renderings, of very little characteristic importance or significance, of shades of difference.

Between the two extremes — submerged aquatic plants and leafless, xerophytic stem-succulents with abundant water-tissue — there is a long graduated series of life-types. It may be stated at once that no *Saxifraga* approaches these two extremes. The habitats of the species differ however fairly widely and therefore the degrees of adaptation are also somewhat variable. The subject may be best viewed by arranging the sections under investigation in a graduated series according to their greater or less xerophytism. Here we may note the very interesting circumstance that species belonging to the same section are fairly uniform in their degree of protection against excessive transpiration: the purely systematic divisions may be extended to include also anatomical and physiological characters. A careful study of the figures shows this fact more completely. The section *Porphyrion* (in casu *S. oppositifolia*) is the most xerophytic, then come the others in the following order: — *Trachyphyllum*, *Euaizonia*, *Dactyloides*, *Nephrophyllum* and *Boraphila*, the two last being almost similar in regard to this feature.

Lastly, if we wish to formulate the results thus obtained (the fact should, however, be particularly emphasized that they are of less importance than the information which may be gathered from the figures), it may be done as follows: —

(1) Each section has its own complex of structural

features in its leaf-anatomy which characterizes the whole group of species; this complex differs in the different sections (as regards its more minute details, see above).

(2) The species cannot, without a certain amount of arbitrariness, all be characterized in common. They show differing degrees of protection against excessive transpiration, from the highly protected species (*S. oppositifolia*, *Aizoon*, *Cotyledon*, *tricuspidata*) to the very slightly protected (e. g. the sections *Nephrophyllum* and *Boraphila*), in exact correspondence with the external conditions of their habitats.

(3) In the few cases in which we know the same species, as regards its leaf-anatomy, both from the Alpine regions of Central Europe and from Arctic regions, the specimens from the Arctic regions show less protection against excessive transpiration than the Alpine (for instance they have not their stomata hidden in "calm" interfoliar spaces, free from air-currents, as Lazniewski found to be the case in Alpine rosette-plants.

(4) Whether there are any differences between the Arctic and the Alpine specimens (besides those pertaining to transpiration) is as yet not known with any certainty, in this paper Arctic specimens, only, having been investigated; Alpine specimens have, it is true, also been investigated, but generally they have been described (and figured) so unsatisfactorily that a comparison would not be entirely reliable. — From the little we know (best from Bonnier and Lazniewski) it appears, however, that in the Arctic leaf there is generally a less decided difference between the spongy parenchyma and the palisade-tissue than in the Alpine, and that the former is

more abundantly provided with intercellular spaces than the latter.

(5) Individuals of the same species appear to vary very slightly in regard to leaf-anatomy, although they may have come from widely separated districts within the Arctic regions.

9.—6.—1910.

5.

Hippuridaceæ, Halorrhagidaceæ and Callitrichaceæ.

By

Agnete Seidelin.

1910.

This investigation is based on the Arctic collections, made by several observers, which are preserved in the Botanical Museum of the Copenhagen University.

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Hippuridaceae.

Hippuris vulgaris L.

Herbarium material from East and West Greenland and Iceland, as also in small quantity from Finmark, Lapland, Nova Zembla and Waigatsch, further, alcohol material from Greenland and Iceland.

In Greenland *Hippuris* is the commonest, phanerogamic water-plant, and it is on the whole the most wide-spread in Arctic regions, according to the reports of botanists. The most northerly place where it has been found is Danmarks Havn, 76°77′ N. L., where it was in the flowering condition when taken by the Danmark Expedition in the month of July (Ostenfeld 1910 p. 29). Mr. Lundager's photograph of the vegetation here which he has kindly allowed me to see, shows it in very shallow water, which is said to have sunk a great deal since the early summer; otherwise it would seem remarkable that the broad, short leaves, which in Denmark are found as a rule under water, are here seen on a large piece of the emerged part of the stalk. The picture also shows with great clearness the slight development of the Arctic plants in comparison with the Danish. Kruuse (1905 p. 151) found it most frequently in water of less

than 30 cm depth, "liable to drying up", Porsild (1902 p. 206), however also in deeper water, 30—70 cm. In "Norges arctiske flora" it is stated, that "it grows most often in localities, where in the earlier part of the summer it lives in water and towards autumn in the air" (Norman 1895 p. 278).

With regard to its growth at Disko, West Greenland ca. 70° N. L., Mr. Porsild has given me the following information.

"*Hippuris* grows preferably in small pools, small depressions in gneiss, often for example no larger than a large bath, so long as they contain water through the whole summer. I have only seen it quite dry once, in the very dry summer of 1909, in a small lake on sandy bottom. It lay there in a curious tangle, but living, with flowers and fruit, and covered the whole bottom.

In larger lakes it forms the outermost belt of the vegetation, outside the *Carex-Equisetum* belt. As there is a predominant wind-direction at each single place, and as this determines the mode of growth, we always find the marsh plants and *Hippuris* on the sheltered side, whilst as a rule there are no plants on the windward side. The seed namely is carried over to the lee side, loose parts of the plants are washed over here, and here there is a "gytje" of dead material of *Nostoc*, of submerged, growing *Hypnum* species and the like, and in this grow *Hippuris*, *Batrachium*, *Callitriche* and *Potamogeton*. The fairly dark material and the dark mosses (e. g. *H. scorpioides*) absorb considerable quantities of heat, and the water is here always much warmer (up to 12°—15° C.) than on the windy side over naked bottom.

In lakes and lagoons with a little brackish water I have never seen *Hippuris*".

According to Lange (1880 p. 13 and 1887 p. 237) and several later authors, the true *H. vulgaris* occurs very seldom in Greenland and most Greenland specimens are referred to v. *maritima* Hartm. (= *H. maritima* Hellen.), though, it is added at several places, with

transitions to the main species. They all seem to me, both the more and less divergent, best regarded as f. *litoralis* Lindberg (1906 p. 109), which only differs from the main form by somewhat shorter and broader leaves (12—17 mm long and 2—3 mm broad), usually 6—8 in a whorl (fig. 1); in the Greenland specimens 9 may occur, according to Krause (1906 p. 224) even 11. The few plants which agree with the description of *H. maritima* Hellen. (1786), or as Lindberg explains, more correctly *H. tetraphylla* L. fil. (1781 p. 81), without however having the characteristic habitus of this, might possibly have developed into f. *litoralis*, the lower parts of the stalk of which may sometimes have short, broad leaves at a height of several dm.

The few specimens I have seen from Finmark, Lapland, Nova Zembla and Waigatsch somewhat resemble the Greenland ones, whereas most of those from Iceland approach more to or are even the typical *H. vulgaris,* thus 10—11-leaved plants from Vallanes, taken in two successive years by Mr. H. Jónsson.

The rhizome forms a sympodium, the structure of which, so far as the material was able to show, agrees with the descriptions in Irmisch (1854 p. 281) and Warming (1884 p. 69). Porsild (1902 p. 206), who gives an account of the occurrence of *Hippuris* on Disko Island in West Greenland, 69°—70° N. L., found the rhizomes about 15 cm down in the mud, in as mentioned 30—70 cm of water, the depth preferred by the plant here, especially in clefts between the rock boulders or between loose stones.

Some plants, among them one found by Jens Vahl "in stagnis sinus Tessarmiut, (= Tasermiut), South Greenland", are richly provided with adventitious roots in the lower leaf-whorls of the upright shoots, like individuals according to Irmisch (1854 p. 287) which grow in damp soil, not in water; yet even in shallow water, which *Hippuris* is said to like in the polar regions, extensive production of roots may occur.

In a basin with shallow water in the Botanical Gardens of

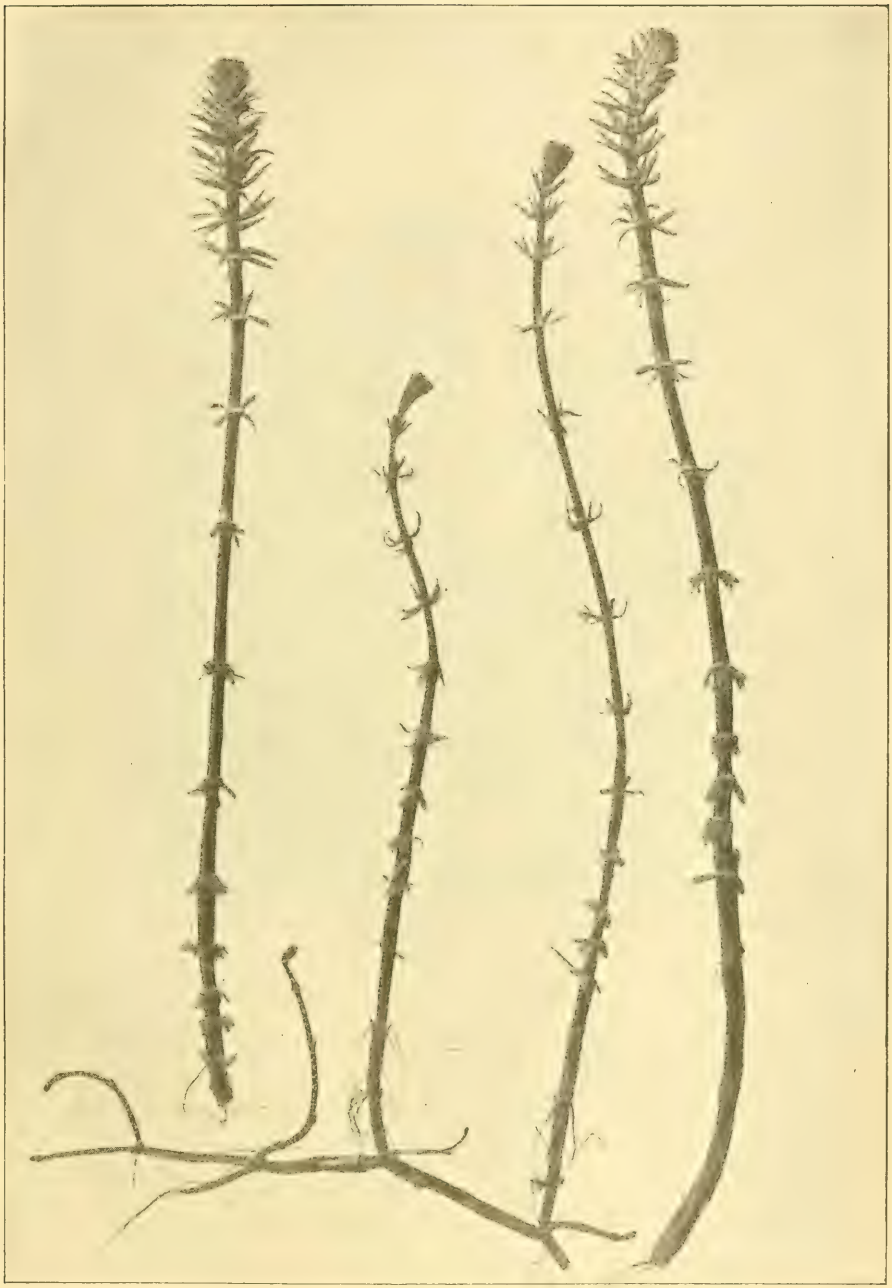

Fig. 1. *Hippuris vulgaris* L. ($^1/_2$ nat. size)
(reprinted from Medd. om Grønland. Bind XLIII. Nr. 1.)

Copenhagen the vertical shoots had an even denser whorl of roots, which however were not very long, but greatly branched; the lowest internode of all was here quite covered by mud. In deeper water in the pond of the Gardens the corresponding shoots had but few roots.

As a rule the roots are unbranched; they are triarch or diarch (fig. 2). The vessels, which are naturally fewer than in the land-form (Schenck 1886 b, Taf. X, fig. 69), gave no wood-reaction in those examined, neither with phloroglucin-hydrochloric-acid nor with potassium permanganate-hydrochloric-ammonia. On Danish specimens examined the red colouration with phloroglucin was extremely faint, not more than observable. It will very probably be more apparent in some specimens. Root-hairs are wanting (Schenck 1886 b p. 58), as in many water and amphibious plants.

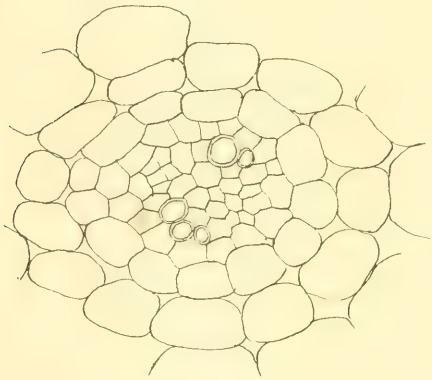

Fig. 2. *Hippuris vulgaris* L.
Root, transverse section.

Transverse sections of the stalk differ from the structure described by Sanio (1865 p. 184) and from that of most of the Danish plants examined, by having fewer — 3 or 2 — circles of large air-canals in contrast to the 5 of Sanio, but they are wider here (fig. 3); the condition is the same whether the section is made across the lower part of the stalk, which would be submerged, or 2—3 cm from the tip, in the flowering, probably emerged part (a very strong specimen from Igaliko 60°—61° N. L.). The most divergent are some small, sterile plants, which I had the opportunity to collect, on an excursion of the Swedish Botanical Society late in July 1909, in a lagoon at Torne Träsk 68°23′ N. L., 342·1 m above the

sea, not within the arctic region strictly speaking, but still in the birch region. In these stalks there are only 2 circles; the fact that *Hippuris* was here growing in the shade of some small bushes, was perhaps not without influence on the structure of the stems. Transverse sections of a herbarium specimen

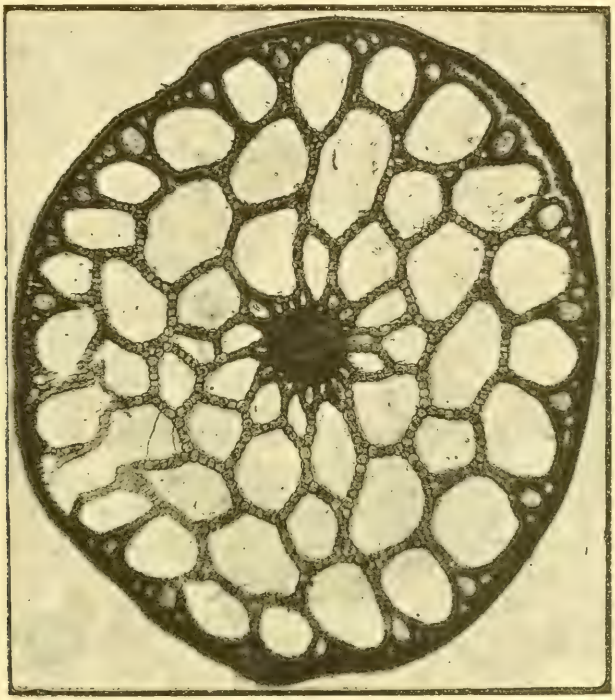

Fig. 3 a. *Hippuris vulgaris* L.
Transverse section of stem. From Greenland.

of *H. tetraphylla* from the Åbo district, Finland, resemble the arctic. Such a structure can also be found in Danish specimens in the submerged portion, whilst the emerged part after an even transition is like that of other Danish plants, and these two stalk-forms can be taken side by side in the same pool. The following seems common in *H. vulgaris*: in the rhizome and lowermost part of the vertical shoot many and small canals,

higher up larger and fewer, then in the upper submerged part and in the aerial part again many and small, though not so marked as in the rhizome.

The outer wall of the epidermis may be rather greatly thickened. The cuticle, coloured red with Sudan III, has fine, longitudinal folds (fig. 4), as can be seen both in arctic and

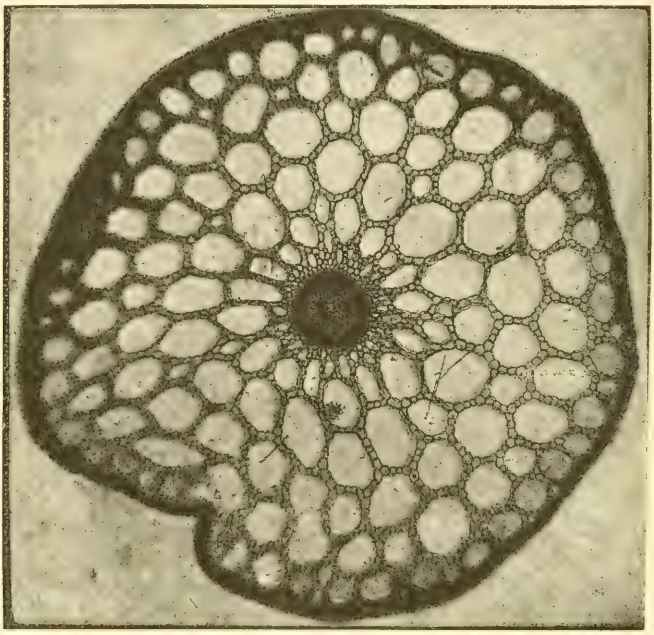

Fig. 3 b. *Hippuris vulgaris* L.
Transverse section of stem. From Denmark.

in fresh, Danish material, where the folds of the submerged part however are indistinct in some cases.

Costantin (1884 p. 317), who has investigated the proportion between the central cylinder and bark in the air stem and water stem in some amphibious plants, gives it for *H. vulgaris* as 0,5 and 0,46; Sernander (1901 p. 170) gives for the bark of the rhizome at least 5 6ths of the diameter. What the condition in this regard is in the arctic *Hippuris* has not been

investigated, as the boundary between the submerged and emerged parts can only be exactly determined at the place of growth. But both in arctic and Danish plants the bark has been relatively greater than given by Costantin.

In longitudinal sections thin sieve tubes can be seen.

Scattered stomata are present on the stalk, as also the characteristic, shield-shaped hairs closely investigated by Rauter (1871). These hairs occur in large quantities on the leaves, especially on the upper side, and in greater numbers on the higher than on the lower leaves.

The leaves appear in three forms with transition-forms.

In the lower, 4—6 leaved whorls they are broad and short without lateral veins and with the mid-vein stopping at the tip without hydathodes (fig. 5 *a, b, c*): they greatly resemble the leaves on some *H. tetraphylla* specimens, on which however I have not made anatomical investigations.

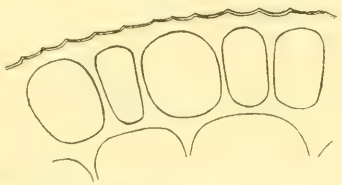

Fig. 4. *Hippuris vulgaris* (× ca. 200). Epidermis of the stem.

The upper leaves, to judge from the Danish specimens air-leaves, and the uppermost water-leaves are longer and narrower (fig. 5 *e*); they have branched lateral veins and prolonged midvein, whose tip which falls off later is provided with hydathodes (fig. 6 *a*) and epithema, in which the spiral tracheids sometimes, but not usually, reach right out to the tip (cf. Borodin 1870). These leaves are dorsiventral, the upper part of the green tissue palissade-like, the lower part with more numerous and larger lacunae, sponge-like (fig. 7) (cf. Clements 1905 fig. 36).

Shoots are present both from Greenland and Iceland, which have the long, narrow, flaccid, submerged leaves but not in the most extreme form from deep water (*B. fluitans* Liljebl. v. *fluviatilis* Hartm.). Porsild (1902 p. 206) observed the usual difference

between "submerged" and "emerged" leaves, between which however as above mentioned, the boundary should not be drawn definitely at the surface, in any case not in Denmark. These ribbon-

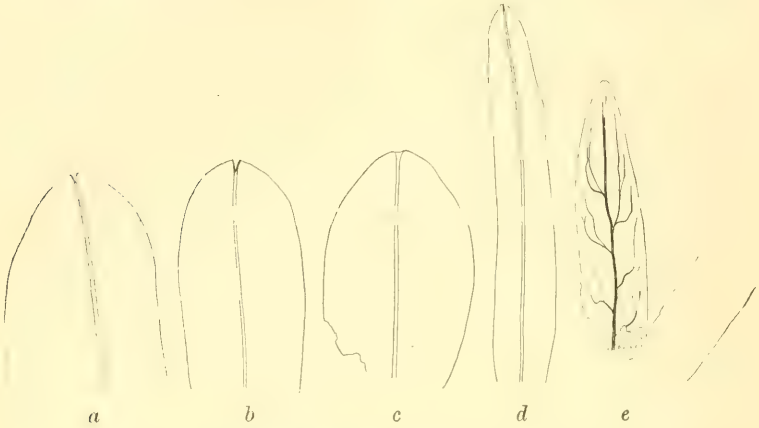

Fig. 5. *Hippuris vulgaris* L. (× ca. 4).
a, *b*, *c* lower leaves. *d* submerged ribbon-leaf. *e* upper leaf.

leaves have no lateral veins, but have hydathodes or they are emarginated after the tip is thrown off (fig. 5 *d*). On transverse sections of them which were examined, only one row was seen

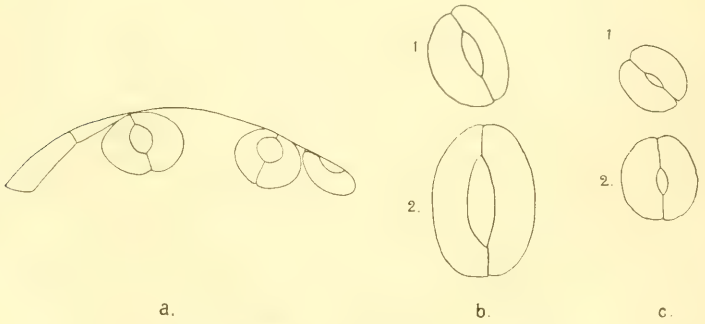

Fig. 6. *Hippuris vulgaris* L. (× ca. 200).
a apex of leaf with hydathodes. *b*, *c* stomata, *b* from upper leaf, *c* from ribbon-leaf.

of large chlorophyll cells between the epidermis of the upper and under sides, which is said to be common by Schindler (1904 p. 75). Some Danish ribbon-leaves had three (cf. Clements

l. c.). The structure of the assimilating tissue varies probably according to the outer conditions of the leaves, especially according to the light directly or indirectly influencing it. The influence of these on the form of the leaf has been studied by Noll (1902 p. 59). In a dark room, which was damp but not steamy, the *Hippuris* leaves, apart from their yellow colour, assumed the appearance of water-leaves without reaching the size of these however, but they did not develop into this form, neither in a dry, dark room nor in a light, almost steamy room.

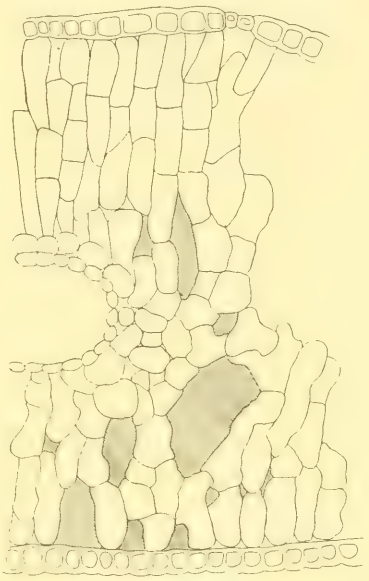

Fig. 7. *Hippuris vulgaris* L. (× ca. 70). Upper leaf, transverse section.

On the ordinary form of leaf there are numerous stomata; as is common among water-plants (Costantin 1884, Schindler 1904) they seem to be present in greater numbers on the upper side than on the under side, both in Arctic and in Danish plants. On the ribbon-leaves they are found only rarely and then but few, and on the short, broad, lower leaves there are only for example 2—4 on a leaf; here they are smaller and with smaller slits than those of the "air-leaves" (cf. figs. 6 *b* and *c*). Porsch (1905 p. 84) found that the stomata in *H. vulgaris L.*, just as in *Callitriche verna L.*, were the reverse of what is usual, as the central slit closed, even on contact with water and under favourable conditions of light.

Flowering, which occurs in July—August in Greenland, in June in some cases in subarctic South Greenland, seems general and occurs even at 76° 77′ N. L., N.-East Greenland; in the

plants from here the flowers occur on a considerable part of the stalk in the axils of flaccid, presumably submerged leaves as well as on the upper leaves.

According to Knuth (1898 p. 411) fertilisation takes place by means of the wind. In the pond of the Botanical Gardens, Copenhagen, however, some fruits were formed on the submerged shoots, which had flowered though less richly than the "air-shoot", down to 10 cm below the surface of the water. Whether these fruit-bearing, submerged shoots have been less submerged during the period of fertilisation, or whether the conditions of fertilisation are different from what is known, must remain an open question.

As the flowers are protogynous (Knuth l. c.), it is difficult to determine from the material, which is for the most part dried, whether in some cases, where only pistils can be seen, the stamens are not at all formed, or whether they are not yet developed. Gynodioecy has several times been observed (Knuth l. c.). Schacht (1850 p. 165) found, that the anthers failed in dry and warm summers; in May he found ♂ flowers, in July ♀ flowers. In the pond of the Botanical Gardens, in the but little sunny summer of 1907, the upper or lower whorls in the flowering part of the stalk of a number of specimens consisted wholly or partly of female flowers. It is possible that they occur in greater quantities in sunny summers. Hellenius (1786) says, that *H. maritima* seems to be always hermaphrodite; neither Linné nor Lindberg mention the flowers in the synonymous *H. tetraphylla*.

Some of the plants were taken with fruit, though the collections do not embrace the whole summer. The fruits are however in general empty. Developed fruits were found in plants from Rode Ö on Scoresby Sound, East Greenland ca. 70° N. L. Hartz (1895 p. 148) describes the region here as having the most copious vegetation he had seen in Scoresby Sound. The bottom of the small lake, which lies ca. 185 m above the

sea, where there are good biological conditions above the fog from the sea and the cold from the icebergs[1], was covered by *Hippuris* and water-mosses. Kruuse (1906 p. 224) states "sets ripe fruit", Angmagsalik ca. 66° N. L., East Greenland.

Vegetative propagation seems predominant here even to a greater degree than in temperate regions. Whether it can proceed here, in addition to by running shoots in the bottom, as Sernander (1901 p. 175) describes, also by means of loose plagiotropic shoots on which are placed orthotropic ones with a kind of hibernaculum, and by means of others with short internodes furnished with compressed leaves, which are formed in the axils of the leaves, or how the spreading from water to water proceeds, is not shown by the material, and just as little the mode of passing the winter. Jonsson (1895 p. 290) on January 10th found the large and small pieces of ice lying on the bank of a large channel at Vallanes, Iceland, densely covered on the downward side with *Hippuris* and *Equisetum limosum*, which were still living and which had earlier been carried away by the ice. At Angmasalik 65°—66° N. L. "the air shoots begin to appear early in June" (Kruuse 1906 p. 224).

Hippuris belongs just as little as *Myriophyllum* and *Callitriche* to the water-plants, whose resistance to the cold has been investigated by Lidforss (1907 p. 47).

It is unknown, how far the rather variable arctic form — or more correctly speaking Greenland form, to judge from the composition of the material — called for practical reasons f. *litoralis* Lindberg, is constant or if it is which is most probable only a reduced *H. vulgaris*, which certainly flowers — even a specimen of only 7—8 cm in height from Angisek, Kitsigsut Islands 59°58′ N. L. Kolderup Rosenvinge (1896 p. 65) — but remains for a long time at an early stage of development in vegetative regards. Often the short, broad leaf-form is retained very long, and on the whole the plant does not attain all the developmental stages, the

[1] According to verbal communication from Dr. N. Hartz.

full number of the leaves nor the usual proportions of size, and with regard to the air-passages remains in the whole length of the stalk like the middle part of some Danish plants. All these questions can only be settled by cultivation of living material, which unfortunately I have not yet had at my disposal.

Nor can we learn without experiment, whether this possible reduction has to be ascribed exclusively to the account of the arctic conditions, or further to the littoral condition which is often added here, and whether both contain factors with the same influence. At any rate there can be no question of the influence of brackish water where Mr. Porsild has seen *Hippuris* on Disco Island (cfr. p. 301).

Halorrhagidaceae.

Myriophyllum alterniflorum DC. and **M. spicatum** L.

Herbarium material from West and East Greenland, Iceland and, for *M. alterniflorum*, the Faeröes; *M. alterniflorum* also in alcohol.

The lower, branched, in the end leafless stems creep rhizome-like in the bottom of still or running water (cf. Irmisch 1859, Warming 1884, Sylvén 1906).

The plagiotropic shoots are chlorophyllous with usually long internodes. *M. alterniflorum* from Kvalböejde, Syderö, the Faeröes, differs from the same species from other localities by having short internodes and being tuft-like; it grew here in shallow water on the sandy west side of the lake, where with other water-plants it came almost right in to the margin, *M. alterniflorum* also in great quantities a little further out (Ostenfeld 1908). Some specimens on the sandy beach of Gurresø, Denmark, have a similar appearance, others not.

From the bases of the leaves descend branched or unbranched roots, as a rule only from the creeping internodes or those just above these, but they may also arise in the upper part of the shoot, above a long, rootless part of the stalk, in specimens

both from Greenland and Iceland. Regarding *M. alterniflorum* from one of the localities Kingua Neriak, Greenland, N. Hartz who found it reports on the label, that it grew "on the bottom of a lake." In Denmark I have observed root-formation in the upper stalk part even when the shoot occurs on the surface of the water, in *M. spicatum* and *M. verticillatum*, at a depth of 2—3 m in Furesø and on a moor, in a trench of slight depth, in August; in the last case roots even sprang from the bracts of the flowers[1]. In running water at Fiskebaek on Furesø both *Myriophyllum* and *Batrachium* had a similar root-formaton, here perhaps deeper in the water. As known, the broken-off shoots of a number of water-plants have the power to develop roots both in the lower and upper parts. Sernander (1901 p. 100) has remarked specially regarding *M. spicatum* that it is found in the autumn "with long roots high up on the shoot".

The branching is generally as Irmisch (1859 p. 354) notes for *M. verticillatum*, shoot-formation from only one of the leaves in a whorl; in *M. alterniflorum* from Friedrichsthal, Greenland, and from a lake at Kobbermine Island at Julianehaab as also from Breidalur, Iceland, 2—4 shoots spring from one leaf-whorl.

The material does not show how the winter is passed; it contains no winter-buds. But at the base of the air-shoot in a number of *M. spicatum* there are leaves which differ from the ordinary by having larger lobes and a somewhat similar appearance to the leaves in hibernacula of Danish *M. verticillatum*. The lateral shoots from the axils of such leaves bear ordinary, finely divided leaves.

As the three *Myriophyllum* species are so difficult to distinguish from one another in the vegetative condition, there might be a possibility in statements regarding the winter-buds in *M. a.* and *M. spic.* of confusion with *M. verticillatum*.

[1] The formation of roots from the nodi of the upper, horizontal part of M. spicatum in running, ca. 1 m deep water is mentioned by O. Rosenberg: Om vaxternas utbildning i rinnande vatten. Svensk bot. tidsskrift. Band I. 1907. Stockholm.

We find such statements in several authors, for example in Koch (1892 p. 865), in Schenck (1886a p. 92), who says that *M. spic.* forms winter-buds, *M. a.* also probably. Birger (1908 p. 57) relies on Schenck's statements when he gives *M. spic.* among the water-plants which form winter-buds further south, but not in Härjedal. Sernander (1901 pp. 184—185) describes hibernacula in both species; in Schindler's diagnosis of *M. spic.* (1905 p. 90) it is said "hibernacula adsunt", whereas they are not named here for *M. a.* In Ferdinandsen and Winge's cultures of *M. a.* at a little below 18° C. (1909 p. 309) no winter-buds were formed. Nor have I found them in this species, when I investigated it in shallow water on the beach of Gurresø in the middle of October 1909, and specimens from here, since cultivated in a room not warmed, have not formed them either, whereas they have been in slow growth through the whole winter and obtained new, weak shoots. Glück (1906 p. 95) concludes from his excursion observations and culture experiments, that these two species are not at all able to form hibernacula.

That the formation of hibernacula might occur in nature by combinations of conditions, which were perhaps not present in experiments even of many different kinds, does not seem impossible, just as that they sometimes appear, sometimes not, dependent on the outer conditions probably, in these species as in *M. verticillatum*, where the time for their formation varies at different places in Denmark at least from August to October. Goebel (1893 p. 361) even found that the formation of winter-buds did not occur "owing to the assimilating activity being too much reduced" at places which were much shaded, but, it must be admitted, that the majority of the plants died here "owing to the cold."

It does not seem excluded that the above mentioned basal leaves belonged to hibernacula, although on the other hand it might well be thought, that the short, polar summer did not offer conditions for their formation, even if we allow that they at all exist.

A strikingly large number of plants are delicate and the lobes of the leaves are fine as hairs, as Schenck (1886 a p. 23) mentions in *Myriophyllums* from very still and small pools.

Abromeit (1899 p. 12) describes specimens from Ikerasak (Umanak region, 70°30′ N. L., West Greenland), taken by Vanhöffen 1899; the leaves have a broad central part and few, but broad lateral lobes or these are absent. A plant of the same material in our possession bears such leaves with lateral lobes on a part of a shoot, whilst the rest of the plant looks like the ordinary *M. spicatum* (fig. 8). The vein of the main part has lateral veins, its tip is bent like a cap but has no marks from the usually occurring and deciduous, trichome-like appendages, which however the lateral lobes show. The leaves examined have no stomata. Abromeit mentions some shield-shaped hairs, and he considers this form to be near to *M. spicatum β heterophyllum* Petermann, whose original description has not been accessible to me[1]. Such hairs I have not seen, possibly because the available material was very scarce. Whether these leaves are formed in the air or under other special outer conditions is not known.

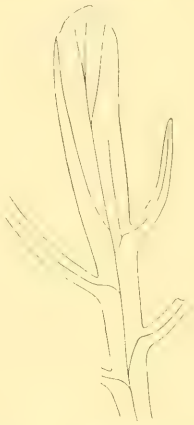

Fig. 8. *Myriophyllum spicatum* L. (× ca. 5).
Leaf of a lateral shoot. (Ikerasak, Umanak, West Greenland). Lateral lobes not finished.

The adventitious roots have a distinct ectodermis. Their woody parts is extremely feebly developed, often only one or 2 vessels in each of the rays, the number of which varies from 2 to 4 within the same order of root, the first one on the same plant. On Schenck's figures (1886 b) a root of *M. spic.* is given as pentarch, whilst its root-branch only has two vessels on the whole; the root of the land-form of *M. α.* is tetrarch. Here as in most of the cases referring

[1] According to Koch (1892 p. 865) *β) heterophyllum* has "die obersten Blätter aufgetaucht (schwimmend) lanzettlinealisch, ganz".

to the anatomy, I have only examined *M. a.*, as only this form was at my disposal in alcohol material.

The structure of the stalk resembles that of *M. spicatum* (Vöchting 1872, Taf. IV); the central cylinder is surrounded by a broad bark with large air-spaces in a circle. In July a large quantity of starch was found in the rhizomic and orthotropic shoots as also in the roots and leaves in slightly brackish water (Melrakke Heath, North Iceland).

Both species may have land forms; the leaves of the latter (Schenck 1884 a p. 22) have dorsiventral lobes in contrast to the radial lobes of the water form; the epidermis of the leaves has no chlorophyll but has stomata, both conditions being the reverse of the submerged form. The stomata in a land form (*M. a*) from a muddy lake-beach, Graenavatn in Iceland (*M. a.*), lie in the longitudinal direction of the leaf section.

Leaves examined of the above-mentioned form, which resemble those of winter-buds, have no stomata.

The section of the submerged leaves has a radial structure and resembles that of the stalk; in principal lobes the air-passages are rather well-developed and arranged in circles, but they are much reduced in very thin leaves; in the lateral lobes they are but few and small and situated irregularly.

Schilling (1894 p. 326) found mucilage formation in the characteristic leaf-hairs of *M. spic.*, in large quantities especially on the winter-buds, the presence of which he thus also recognizes. Other points of the shoot are also enveloped in mucilage from the surrounding leaves. On older leaves only the brown scars from the deciduous trichomes are seen.

According to Parmentier (1897 p. 138) and Schindler (1904 p. 53) *M. spicatum* is distinguished from most other species by having calcium oxalate crystals only in the stalk, not in the leaves. They also occur in the leaves however of specimens both from Greenland and Iceland, and from Denmark (determined by Dr. A. K. Schindler), though in smaller quantity than in *M.*

alterniflorum and *M. verticillatum*. The plants examined were taken in July and August.

Both species flower in July—September, *M. spicatum* taken by Vanhöffen at 70°30′ N. L. on July 18 (Abromeit 1899 p. 12).

Myriophyllum is monoecious. Warming (1886 p. 116) gives *M. a.* and *M. spic.* among the anemophilous plants of Greenland (cf. Knuth 1898 p. 309). So far as I know, water-pollination has not been noted for these two species as for *M. verticillatum* (Ludwig 1881 p. 10). Abromeit (l. c.) observed distinct protogyny in *M. spicatum*, in the Umanak Fjord district, but further, that the pollen is emptied already in half-opened ♂ flowers. Schindler (1905 p. 14) remarks, that the lowermost, first opened flowers of several Myriophyllum species are wholly female.

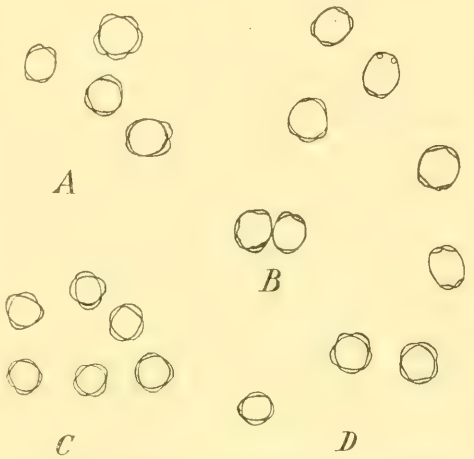

Fig. 9. *Myriophyllum*. Pollen (× ca. 100). *A* and *B* M. alterniflorum DC. *A* Danish, *B* Arctic. *C* M. verticillatum L. *D* M. spicatum L.

The pollen grains of *M. alterniflorum* (fig. 9), both in arctic and Danish specimens, differ from those of *M. spicatum* and *M. verticillatum* as described and figured by Mohl (1834 p. 331). The pores of the pollen, usually 4, are placed 2 near one another at the one pole, 2 at the other, and not with the same distance between all 4 as in the other species. 2, 3 and 5 may also occur; 5 may also be found in *M. spicatum*, just as we sometimes see transitional forms with regard to the distance between the pores.

The outgrowths mentioned in Schindler's description (1905 p. 94) as occurring on the ovary of *M. a.*, give with vanillin

and hydrochloric acid (Raciborski 1893) the reaction for myriophyllin, which was found by the latter in the leaf-appendages; on the ovarial outgrowths it is however less purely red in colour than from the leaf-appendages, more brownish red.

M. a. has formed fruits at several places, in Greenland (Septbr.) at Tunugdliarfik, 60°50′ N. L., in Iceland (Aug.) among other places at Breidalur; fruits from here have developed embryos. The small quantity of fruit in the material is possibly due, for *Myriophyllum* as for *Hippuris*, to the fact, that the collections were in general not made in the autumn.

Sylvén (l. c.) has only described and figured seedlings of *M. a.*

Vegetative propagation probably occurs readily, even if the winter-buds are not found, on detached parts of shoots as in other regions (Sernander 1901; Glück 1906 etc.).

M. alterniflorum is on the whole a more northerly species than *M. spicatum*, and a greater number of specimens have been collected than of the latter. Both species have generally a more slender appearance than is common in Denmark, possibly connected with the less favourable conditions of life; this refers less to *M. a.* which is a slender species in any case. The Greenland specimens of this species are not so strong as those from Iceland, but there are only 3 individuals from the latter country.

Callitrichaceae.

Material from East and West Greenland, Iceland and the Færöes together with a very few samples from Finmark.

The following species have been found: *C. autumnalis* L., *C. hamulata* Ktz., *C. stagnalis* Scop. and *C. verna* L.

C. stagnalis which is a species belonging to the temperate and warm regions e. g. found at Ceylon (Hegelm. 1864, p. 59, Schenck 1886 a p. 151) has not been gathered in Greenland and

in Iceland only in the surroundings of hot springs, thus at Laugarne near Reykjavik in water of a temperature of ca. 25° (Gronlund 1890 p. 140, Ostenfeld 1899 p. 238, Stefansson 1901 p. 117); the ubiquitous *C. verna* not with certainty on the Færöes. In Greenland *C. verna* was found as far up the mountains as ca. 166 m. above the sea, in Scoresby Sund ca. 70°15′ N. L., East Greenland (Hartz 1895 p. 323). Hegelmaier notes it from the Morteratsch glacier, Engadin (l. c.).

C. polymorpha Lönnr. is mentioned from Greenland, but as far as I am able to judge, this species consists of forms of other species, viz. of *C. verna* and *C. hamulata*.

C. autumnalis, gathered only a few times, has a low growth, especially the species from Disco, West Greenland, ca. 70° N. L., found by M. P. Porsild in a depth of 0,16—0,33 m, but those from Iceland too; from the Færöes there is but little material of this species. It is only available in herbarium-specimens, and for that reason not examined anatomically.

Some peculiar plants gathered by Professor Warming July 6, 1885, in the river Alten, Finmark, appear to be *C. longistyla* Norman (1895 p. 281), who has noted it only from one locality, near to the same river at Raipas about 69°57 N. L.

Callitriche is found in still as well as in running water, *C. verna* also in dried-up places (e. g. Norman l. c. p. 280), which seems to be comparatively often the case in Greenland.

C. autumnalis in lakes at Disco, ca. 70° N. L. (Porsild 1902 p. 206), was growing in patches together with *Batrachium paucistamineum* and aquatic mosses, in shallow water as mentioned above. On the Færöes *C. hamulata* occurs mostly as landform, but also grows in the *Litorella*-association in lakes, and in streams (Ostenfeld 1901 p. 57, 1908 p. 140—142).

The bottom in which seedlings of *C. verna* were observed in a lake on Danmarks Island (70°27′ N. L., East Greenland, Hartz 1895 p. 278) consisted of gytje. It was sandy and muddy in a pond with about 35 cm water, in which *C. hamulata* Ktz.

var. *trichophylla* Ktz. was growing, 3—10 cm high, with fruit, Septbr. 30. 1901, Angmagsalik, 65°37′ N. L. (Kruuse 1906 p. 224).

The habitus of the different species, if living in water, is very similar, small plants with slender branching stems and opposite leaves, the uppermost of these, except in *C. autumnalis*, forming a rosette on the emerged part of the stem. When living in dry places *C. verna* is short and branches abundantly, looking tuftlike, often it is prostrate (cfr. *f. minima* Hoppe and *f. caespitosa* Schultz). The forms, however, vary very much and do not always correspond to the description.

Most likely the species of *Callitriche* in arctic as well as in temperate regions are as a rule perennial without making special winter-buds (Irmisch 1859 p. 354; Schenck 1886a p. 84; Warming 1884 p. 90; Sylvén 1906 p. 187; Birger 1908 p. 57). H. Jonsson (1895 p. 290) observed lots of *C. hamulata* in a slowly streaming channel, Vallanes, Iceland, Jan. 10; the water had been frozen from the beginning of Novbr. until Decbr. 28. That *Callitriche* is able to live below the ice during the winter is often seen, e. g. *C. verna* in the Botanical Gardens of Copenhagen and in ditches near Fureso, but how it hibernates if the water is frozen to the bottom, seems not to have been investigated; perhaps at least parts of the stem will survive even then (cf. p. 332).

The observation that species of *Callitriche* are annual (e. g. Hartmann 1879 p. 383; Neumann 1901 p. 307—308) probably applies only to the terrestrial forms. Such is the case according to Irmisch (l. c.) and Sylvén (l. c.). Ostenfeld (1908 p. 938) writes that occasionally *C. hamulata* is annual on the Færöes; i. e. when the plant grows on land, according to verbal information of the author.

The primary root is succeeded by adventitious roots.

The ability of the nodes to form roots is very great. They are short and rather stout in many of the land-plants, long and slender in aquatic ones. They may be found, just as sometimes in *Myriophyllum*, even at the nodes bearing flowers.

The roots are furnished with root-hairs, but rather sparingly; the latter condition seems quite natural with aquatic plants, which are often quite devoid of them, but it is also the case in the terrestrial specimens (*C. verna* and *C. stagnalis* examined).

Generally the roots are not branching. In a few cases one to four branches have been noticed e. g. in *C. verna* from a dried-up pool at the settlement Ingnukertok (in Angmagsalikfjord, Greenland 65°45′ N. Lat.) and in *C. hamulata* from a river at Miavevatn, the Færöes, gathered by C. H. Ostenfeld. The slender roots of the latter indicate, that the plant has been submerged; it cannot with certainty be seen whether parts of them have grown on the bottom. According to Lebel (1863) p. 4) it was only in the latter case that the roots were branching; Hegelmaier (1864 p. 29) looked in vain for branching roots though, as is added, not to any great extent. Schenck (1886 b p. 60) describes the root as not ramiferous.

The central cylinder is the most simply built of the Dicotyledons, being diarch (*C. stagnalis*, aquatic form) or triarch (*C. stagnalis*, terrestrial form and *C. verna*) (Schenck l. c.) as in *Hippuris vulgaris*, but with less numerous vessels than this plant. The arctic roots examined agree in all essentials with the description of Schenck.

The stem, if submerged is thin and the internodes long, if growing on damp places thicker with shorter internodes, partly prostrate and sending out roots.

The anatomy is that characteristic of several aquatic plants. Below a thin epidermis without chlorophyll is a thick bark, with large air-channels. The parenchyma contains chlorophyll, in older plants it is partly resorbed. The endodermis as in a root is sharply marked off towards the central cylinder.

Hadrom and leptom are only slightly developed. As pointed out by Hegelmaier (1864 p. 20) the number of the vessels vary within the species being dependent on the nutritious conditions. The following numbers will give an idea of the variability.

C. verna, a land specimen from a dried-up pool, Røde Ö East Greenland c. 71° N. L., had 4—6 vessels in the upper internodes; in a basin in the Botanical Garden of Copenhagen 5, in a part of the stem 6—7 internodes below the top. *C. hamulata* from Miavevatn, the Færöes, has 7, while in the figure of Hegelmaier (l. c.), only two are seen. In *C. stagnalis* from Laugarne, Reykjavik, Iceland, 16 are found, in a part of the stem furnished with stomata and pith, indicating emerged situation; Hegelmaier and Schenck mention, that 12 may be found, which number was seen in a robust specimen from Kunø, the Færöes; the figures of Schenck and of Hegelmaier show 7 and 11 in the land form, 4 and 7 in the aquatic form (1886 b and l. c.).

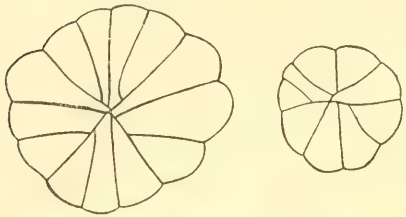

Fig. 10. *Callitriche hamulata* Ktz. (× ca. 150). Hairs from leaf and stem.

Either very little pith is present or in its place in the centre of the stem, only a canal, the young pith-cells, when only very few, having burst with the stretching of the surrounding tissue (Hegelm l. c. p. 20). On an average the pith is less resorbed in terrestrial forms than in aquatic ones.

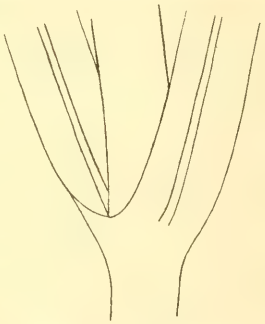

Fig. 11. *Callitriche hamulata* Ktz. (× ca. 10). Base of the leaves.

The stem and both sides of the leaves, in the species belonging to *Eucallitriche*, bear shield-shaped hairs (fig. 10), resembling those of *Hippuris*, abundantly on the air shoots or upper part of the submerged ones, very few on the lower part.

The opposite leaves connate at the base (fig. 11).

With exception of *C. autumnalis*, belonging to *Pseudocallitriche*, the species have polymorphous leaves with transitional forms.

The short and brod obovate form in the rosette of *C. verna* is strikingly different from the linear one, which is deeply submerged.

In *C. hamulata* some of the emerged leaves and the upper submerged are shortly spatulate, below these longer spatulate and sublinear ones are found, the narrowly linear leaf closing the series (fig. 15 and 12).

Most specimens of *C. stagnalis* have typically broad leaves, yet diminishing in breadth downwards, e. g. in plants from a ditch at Vaags Ejde lake, the Færöes, July 23, 1897 (C. H. Ostenfeld). The form *platycarpa* Ktz. from deeper water has not been found in the arctic material.

The leaves of *C. autumnalis* as well as those of other *Pseudocallitriche* are uniform and linear.

Fig. 12. *Callitriche hamulata* Ktz. (× ca. 5). *A* upper leaf, *B, C* lower leaves.

Most of the submerged leaves may be classed in the elodioid type of Warming (1909 p. 182) or are somewhat longer.

Fig. 13. *Callitriche verna* L. (× ca. 15). Terrestrial form.

The apex of the leaf is in varying degree emarginate; the two points are straight if short, but converging if longer. More rarely the leaf is almost evenly truncate (fig. 14 *c*, *d*). In the small leaves of the terrestrial form of *C. verna* the apex is rounded (fig. 13).

Very deeply emarginate are the exceedingly long and narrow leaves of *C. hamulata f. trichophylla* Ktz. (fig. 14 *e*, *f*), e. g. gathered at Sukkertoppen 65°25′ N. L. Greenland, and at Bjørnedal near Ivigtut 61°13′ N. L. Greenland, moreover those of the robust, relatively

broader leaves of the already mentioned specimens from Vallanes, Iceland.

The venation is very simple. In the broader leaves three or five veins, in most of the narrow leaves only a single one, while in others and in transition-forms three or one with lateral veins only in the upper part of the leaf, generally making a sharp curve towards the median vein at the beginning and ending. Sometimes parts of them do not meet, either the middle part or those next to the midvein being absent (fig. 12 *C*).

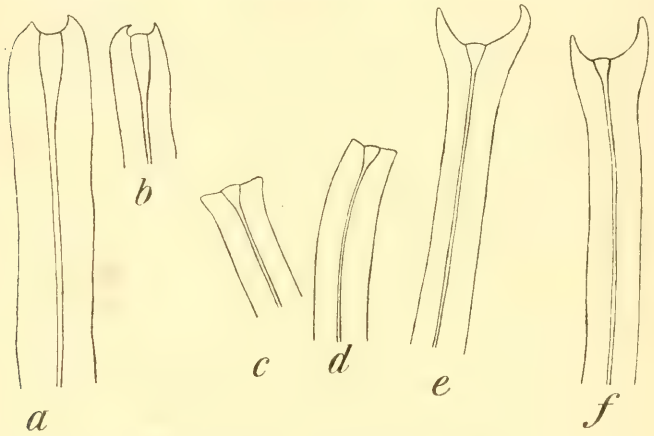

Fig. 14. *Apex of the leaf.* (× ca. 5).
a, *b* Callitriche verna L. *c*—*d* Callitriche hamulata Ktz. *d* upper leaves. *e*, *f* lower leaves.

According to Hegelmaier (1864 p. 32) the former are generally formed first, but sometimes the formation of the lateral vein begins in the middle part quite without connection with the mid-vein.

A few communicating small veins may be found.

It is remarkable, that the small leaves of *C. verna* terrestrial form, have only one vein, perhaps with a few indistinct branches, the venation of amphibious plants generally obtaining the richest development in emerged leaves. Possibly this is, in one way or another, connected with the form of the leaf.

Beneath the broad apical part of the median vein, opening

on the under side of the leaf is a big hydathode (Borodin 1870 p. 841 and fig. 1—5), developed both in air-leaves and in water-leaves.

The dorsiventral condition is distinct in the upper leaves, but gradually grows very indistinct downwards, the lowest leaves of submerged stems are almost isolateral.

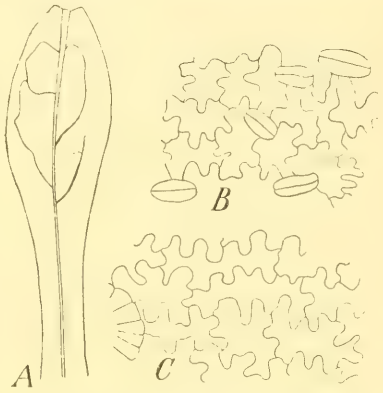

Fig. 15. *Callitriche hamulata* Ktz. *A* one of the uppermost leaves (× ca. 5). *B* upper, *C* lower epidermis of a leaf like *A* (× ca. 70).

It need hardly be said, that the outer wall of the epidermis is thicker in air-leaves than in water-leaves. The epidermis does not contain any chlorophyll as does that of many other aquatic and amphibious plants. The cells have undulating walls and are nearly isodiametrical in the short and broad leaves; the undulation gradually grows less marked and at last wholly disappears, the cells becoming more and more oblong, as the leaves gradually decrease in breadth downwards (cf. fig. 15 and 16). The drawings represent cells from the middle part of the leaves, placed between the mid-vein and the border. Near the apex the cells are in the main shorter and the walls more undulated than in the middle of the leaf, and near the base they are longer and narrower and often straight-walled. The cells above and below the mid-vein and near the border also differ, namely, in being rather long and not or only slightly undulated.

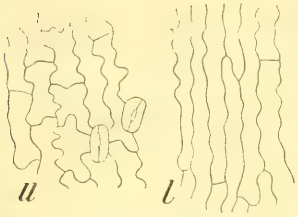

Fig. 16. *Callitriche hamulata.* Ktz. (× ca. 70). *u* upper, *l* lower epidermis of the leaf fig. 12 *C*.

The lower epidermis generally appears less well developed

than the upper one, the cells being longer and the walls less distinctly undulating. The lower surface of an upper leaf may often have the same appearance as the upper surface of one placed lower down.

In *Callitriche* as in many other aquatic plants only the upper epidermis is furnished with stomata, except in some cases in emerged leaves, in which they also may be found on the lower (fig. 15 and 16).

They are numerous, as is to be expected in air-leaves and perhaps also in upper water-leaves, few or none in deeper submerged ones. Sometimes they are deformed. As mentioned above (cf. p. 309) Porsch (1905 p. 84) observed, that the stomata of *C. verna* behave differently to other stomata, closing if in contact with water and under favourable conditions of light.

The structure of the chlorenchyma agrees in the main with the drawings and the descriptions of Hegelmaier (1864 p. 31) and Schenck (1886 b p. 19). The leaves in some cases are more highly differentiated than those represented by these authors. The palissade-tissue of a plant of *C. verna*, which is apparently the terrestrial form (Mudderbugten, Greenland ca. 70°15′ N. lat., N. Hartz Aug. 30.), as well as that of an upper leaf of *C. stagnalis* (Laugarne, Reykjavik, Iceland, C. H. Ostenfeld Aug. 7, 1895), is more developed than in the "land-leaf" of *C. verna* (Schenck l. c.), while the structure of another leaf, about 6 cm lower down on the stem of the same specimen of *C. stagnalis*, is almost like the drawing.

Some linear leaves, deeply emarginate at apex, of *C. hamulata* (Sukkertoppen, Greenland 65°25′ N. L., 16. August 1884) are a little more reduced than in any mentioned by these authors. The upper one of the three or only two layers of chlorenchyma cells are more rounded, of an almost isodiametrical. i. e. more primary shape, only incompletely developed (Fig. 17), the intercellular spaces are larger, while the vascular bundle and its starch-sheath are less developed.

As the anatomy of aquatic-plants varies exceedingly within the species, influenced as they are by the very variable conditions to which they are exposed, no great importance should be attached to these smaller differences, the value of which can not be measured without intimate knowledge of local conditions.

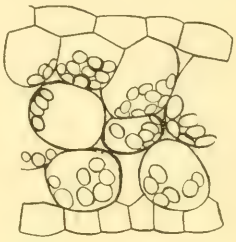

Fig. 17. *Callitriche hamulata* (× ca. 165). Transverse section, middle of leaf. Starch is seen.

As is quite natural, because of the more intense assimilation, in some cases much more starch is found in the short and broad leaves than in the narrow leaves, often quite filling up the chlorenchyma cells of the former.

Callitriche develops flowers and fruits in abundance in arctic countries; only a few specimens of the material are devoid of flowers. Both are found at the same time generally, except of course in the beginning of the summer, when only the very first flowers are present.

	Greenland		Iceland	
	only flowers	fruiting	only flowers	fruiting
C. autumnalis.		Aug.		July
C. hamulata.	June—July	Aug.—Septbr.	June—January	July—Aug.
C. stagnalis.				July—Aug.
C. verna.		July—Septbr.		July—Aug.

	The Færöes		Danmark
	only flowers	fruiting	flowering (Raunkiær, 1906)
C. autumnalis.			July—Septb.
C. hamulata.		July—Aug.	May—Septb.
C. stagnalis.		July—Aug.—Novb. 4.	May—Septb.
C. verna.			May—Septb.

The flowering period is thus in the main as was to be expected, somewhat later than in temperate regions. Very likely fruits and perhaps flowers might be found later in the year than Aug.—Septb., but as mentioned before, most travellers

have finished collecting at that time. The material of *C. stagnalis* from Kvannasund (the Færöes) Novb. 4. still contains fruits *in situ* and even that of *C. hamulata* from Vallanes, Iceland, January 10 (cf. p. 320), bears both pistillate and staminate flowers; both have been gathered by H. Jonsson.

The monoecious flowers are placed in the axil, ordinarily one flower in each of them; in some cases a staminate and a pistillate flower are found in the same axil.

Fig. 18. *Callitriche longistyla* Norman? (Alten, Finmark) (× ca. 8). *a* staminate flower. *b* pistillate flower.

The arrangement is often the following (cf. Hegelmaier 1864 p. 36); low on the stem, i. e. early developed, pistillate flowers, higher on the stem, i. e. later developed, staminate ones and in the middle part a pistillate flower in one corner and a staminate flower in the other corner of the same pair of leaves, e. g. in *C. hamulata* from a river, Bjørnedal at Ivigtut, South Greenland.

The pollen from the only stamen of the male-flower is transported to the two long and thin stigmas, covered in most part of the length with oblong papillæ, by the wind according to Knuth and other authors, while some authors suppose hydrophily and entomophily to take place.

The stigmas of the above-mentioned form from Alten, Finmark — possibly *C. longistyla*, Norman — are exceedingly long (Fig. 18).

The stigmas of the flowers of *C. stagnalis* (gathered by C. H. Ostenfeld at Laugarne near Reykjavik, Iceland, Aug. 7. 1895, are longer than the fruit, while those of other flowers were shorter or of the same length as the fruit, as is common in this species. Warnstorff (1896 p. 27) observed flowers with

such long stigmas on lateral shoots and supposed them to be fecundated below water, though he had not then found submerged male flowers.

Knuth (1899 p. 380) and Warnstorff (1896 p. 27) describe *C. verna* and *C. stagnalis* as anemophilous and protogynous, speaking of the sprout; in the small inflorescence of the axil, found in strong and well nourished specimens of these two species, the male flower is earlier developed than the female one, Hegelmaier (1864 p. 35); according to Ludwig (1881 p. 9) they are hydro-entomophilous.

In contradiction to this Hegelmaier (1864 p. 59) found *C. stagnalis* sterile, if quite submerged, and he supposes that such is also the case with *C. hamulata* (l. c. p. 56). According to Kerner[1] "the stamen of these flowers did not open at all". In Botany of the Færöes Ostenfeld (1908 p. 938) writes of *C. hamulata*, that it is pollinated by the wind but capable of self pollination, when the water is high and the flowers submerged, this accounting for the regularity of fruiting. Some plants of this species from Mödruvellir and from Vallanes, Iceland, bear fruits; only linear leaves being present, the plants have probably been submerged. In a fruit from Vallanes, placed in the axil of a deeply emarginate leaf, 8·5 cm. from the top of the shoot, the embryos were developed, which shows, as far as might be concluded from a herbarium specimen, that Hegelmaier is not right in supposing that submerged fruiting does not take place.

The fecundation of the more simply built flowers of *C. autumnalis* as well as those of other *Pseudocallitriche* is effected below the water. It has been studied by Jönsson (1884 p. 21); the pollen, the specific gravity of which is less than that of the water, is filled with oil.

As in temperate regions the abundance of fruits is largest

[1] quoted from Knuth's Blüthenbiologie.

in terrestrial plants, but even in shoots which appear to have been submerged, e. g. from Iceland (Aug. 24. 1894, Ol. Davidsson), three fruits to one pair of leaves, i. e. two in one of the axils, may be found.

Some of the plants of *C. hamulata* (from Godthaab, West-Greenland 64° 11′ N. L. Septb. 31. 1907, dr. Soren Hansen) are only 2 cm. long and yet fruiting; also in the small specimens of *C. autumnalis*, 1·3—3·2 cm. long, from shallow water, only c. 0·33 m. deep, from a lake in West-Greenland (Hammersdal, Disco 70° 9′ N. L., M. P. Porsild) fruits are present. Irmisch (1859 p. 354) observed flowers in the first pair of leaves of *C. verna*, both on the primary stem and on the shoot from the cotyledonary axil.

Fig. 19. *Callitriche verna L.* (× ca. 16) Embryo.

As a rule all parts of the quadrisulcate separating fruit have been developed, all of them containing an embryo (fig. 19). Sometimes only two or three parts have been developed, e. g. in *C. stagnalis* from Laugarne (at Reykjavik, Iceland, C. H. Ostenfeld Aug. 7. 1895) this is rather common.

The material of *C. autumnalis* being very small and only herbarium specimens, only a few fruits have been examined; some of these contain three embryos; thus they do not correspond to v. *lunulifera* Norm. from the farthest North (Hartman p. 383) with only two separating fruits developing. Judging from the abundance of well-developed embryos, seedlings should be expected to be very common; Hartz (1895 p. 278) found *C. verna β minima* only as seedlings in the middle of July in an early ice-free lake on Danmarks Ø 70° 27′ N. L., East Greenland. Some of the specimens of the material are seedlings.

But vegetative propagation is probably frequent in the far North as well as in the temperate zone, where (Sernander 1901 p. 157 etc.) many shoots are set free all the year round in water free of ice.

If cultivated they grow and roots are developed even on very small pieces. "In *C. autumnalis* the vegetative propagation might be less important than in the other species. The vegetative shoots, however, with their air-channels act as an excellent floating apparatus for the heavy fruits, which, if isolated, immediately sink to the bottom. Within the other species too the fruits are generally carried with the mother-plant" (Sernander). Kolpin Ravn had also observed (1894 p. 178), that the fruits of *C. autumnalis* were unable of themselves to float. Thus their wings are in that respect of no use.

Isolated seedlings of *C. stagnalis* were found among the flotsam in the course of the summer in Sweden (Sernander l. c. p. 157 and 82).

Summary.

As was to be expected the plants examined, being aquatic plants, show no morphological or other peculiarities except in size, which could with certainty be referred to arctic conditions. Aquatic plants as is well known are subject to great variations, such variations being very dependent on external conditions, probably mainly of a nutritious nature, as has especially been pointed out by Goebel (1893, 1908 etc.) and Küster (1903). This being granted, it seems natural, that these variations largely depend on light conditions, — seen for instance in the differences between specimens from deep and from shallow water —, because of the assimilation which does not preclude the light from also in other ways having effect on the variations.

Thus, the numerous small differences met with may be due only to local circumstances.

But in size the specimens from Greenland are on the whole smaller, both those of *Hippuris*, *Myriophyllum* and *Callitriche*

— and the specimens of *M. spicatum* and *Callitriche* are also less robust than those from Iceland and the Færöes, which show no obvious differences from plants from other temperate regions. The shorter period of vegetation might suffice to explain the smaller size, but in the case of the robustness, e. g. of the leaves, other circumstances must also be active, very likely amongst others temperature of the water. But investigations relative to this must be carried out on the spot and combined with experiments.

Whether the quantitative peculiarities of *Hippuris* from Greenland — the smaller number and the relatively greater breadth of the leaves together with the fewer circles of air-channels of the stem — which features might possibly all be regarded as reduction — are constant characters, the arctic *Hippuris* thus being a special systematic form, or whether they would alter if exposed to other circumstances, can be decided only by investigations on living and cultivated plants.

My best thanks are due to Professor Warming for the kind interest taken in this work, to Dr. C. H. Ostenfeld for various, especially phytogeographical items of information and for having controlled the determination of some species, further to the Director of the Danish arctic station at Disco, mag. sc. M. P. Porsild for the above-quoted notes on the biology of *Hippuris* in Greenland and for several other communications.

Additional Note. About *C. autumnalis* mag. sc. Porsild has given me the following information. "It was growing on gytje on the lee-side of a shallow pond, the windward side being without vegetation. It must be supposed to remain frozen in the ice from the beginning of Octbr. until late in May, when the ice melts at the border, while in the middle it remains until late in June, at least".

20.—6.—1910.

6.

Ranunculaceæ.

By

Knud Jessen.

1911.

The subject-matter of the present paper has been worked out in the Botanical Laboratory in Copenhagen and my thanks are due to Professor Warming for his great kindness in giving me advice and help. I have used his notes of his Arctic journeys, and I am indebted to him for most of the flower-biology drawings and some others. As regards the remaining figures, the anatomical ones have been drawn by me and most of the morphological ones have been drawn under my supervision. The spirit-collection of *Ranunculaceæ* belonging to the museums of Copenhagen and Stockholm, in which most of the species are richly represented, were freely placed at my disposal and for this I wish to express my gratitude to the Directors of the museums, Professor Warming and Professor Lindman. I have also been kindly permitted to use the Arctic herbarium belonging to the Botanical Museum in Copenhagen. In addition I wish to express my thanks to the Inspector of the Museum, Dr. phil. C. H. Ostenfeld, for the kind help I have several times received from him.

The following species have been investigated: —

Anemone Richardsoni . . . . . p. 414
Batrachium confervoides . . . . . p. 410
Coptis trifolia . . . . . p. 426
Ranunculus acer . . . . . p. 354
— *affinis* . . . . . p. 349
— *glacialis* . . . . . p. 338
— *hyperboreus* . . . . . p. 392
— *lapponicus* . . . . . p. 397
— *nivalis* . . . . . p. 373
— *Pallasii* . . . . . p. 404
— *pygmæus* . . . . . p. 380
— *reptans* . . . . . p. 387
— *sulphureus* . . . . . p. 364
Thalictrum alpinum . . . . . p. 419

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Ranunculus glacialis L.

Wydler, 1859, p. 263. Lindman, 1887, pp. 19, 25, 39, 99, tab. I, fig. 6. Wagner, 1892, p. 55. Norman, 1895, pp. 1—4. Kerner, II, 1898, pp. 162, 272, 276. Andersson & Hesselman, 1900, p, 42. Resvoll, 1900, figs. 1, 6, 10, 16, 17. Cleve, Astrid, 1901, p. 50. Dusén, 1901, p. 29. Freidenfelt, 1904, p. 54. Sylvén, N., 1905, pp. 134—40, fig. Hollstein, 1907, pp. 84—85, 88.

Alcohol material from Flojfjæld (Tromsø), 23. 7. 1885; Knudshø (Dovre), 7. 1891; Jan Mayen, 22. 7. 1896.

The rhizome is vertical or oblique and remains alive for several years; the length of the longest I measured was about 5 cm. The primary root dies early, and afterwards only adventitious roots occur. The latter arise without apparent order from the entire surface of the rhizome; withered leaf-fragments and a few short hairs occur between the roots.

Hollstein records that the rhizome is exceedingly short and that it dies at the same time as the floral-axis produced by it; consequently upon this point there appears to be a difference between the Arctic individuals of the species examined by me and those from Central Europe.

When flowering begins, the rhizome becomes sympodial with, usually, only one branch from the uppermost of the leaf-axils at the base of the stem; but specimens often occur with 2-several growing-points on the rhizomes, consequent upon the fact that other leaves of the rosette, besides the uppermost, may subtend buds. The flowering-axis usually bears only a few leaves at the base, viz. on the outside 1—3 scale-leaves with large sheaths and rudimentary laminæ, and then, 1—2 (according to Wydler as many as 4) long-stalked foliage-leaves; the leaf-spiral is $\frac{2}{5}$. In the majority of the specimens examined by me these foliage-leaves were wanting and the principal bud was therefore situated in the axil of the upper-

most scale-leaf (Fig. 1). Sometimes forms transitional between scale-and foliage-leaves occur. In the spring the principal bud develops into a leaf-rosette consisting entirely of stalked foliage-leaves, of which the first two (or according to WYDLER the first 2—4) stand transversely with regard to the subtending leaf and the parent-axis, while the others succeed in a $^2/_5$ spiral; later in the year the scale-leaves must be developed, and the plant probably passes the winter with a winter-bud covered by the scale-leaves.

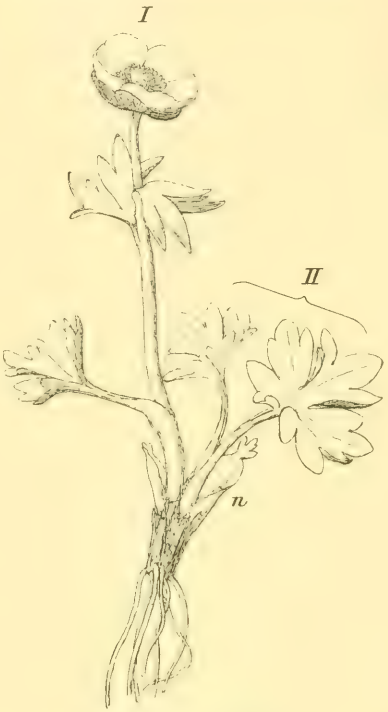

Fig. 1. *R. glacialis.*
(Trömsö; about nat. size). I, Main axis; II, principal bud, *n* its subtending leaf.

The more-or-less erect, rounded and almost glabrous flower-stem bears 1—4 leaves of which the lower are stalked and the upper are sessile. The radical leaves and the stalked stem-leaves are almost similar in form, somewhat reniform, and palmatipartite, with broad primary segments; the sessile stem-leaves are divided in a similar manner; but the segments are lanceolate-elliptical. All the leaves are somewhat fleshy and are slightly hairy upon their lower surface.

The lower stem-leaf may subtend a vegetative bud which, like the principal bud, bears first two transversely-placed leaves. According to WYDLER, this bud may effect vegetative propagation because the parent-stem lies prostrate upon the ground, while the bud strikes adventitious roots and becomes fixed thereby.

The herbarium-specimens in the Museum of Copenhagen confirmed this only in so far as that several stems appeared to have been prostrate to a greater or lesser degree. The 2—3 upper stem-leaves may subtend floral-axes, which each bear from one to two lateral green bracteoles. Between the principal axis and the lateral axes there is sometimes antidromy, sometimes homodromy. — The principal bud, in each of the few Greenland plants preserved in spirit, was only about 2 mm. long while, in the specimens from the other localities it always had several fully-developed leaves; all were gathered at the same time, the middle of July.

Fig. 2. *R. glacialis.* Almost ripe fruit from the Færöes, 21. 8. 1897 (about 5/1). Herbarium-material); *sem.*, seed.

The non-flowering specimens grow monopodially and have a terminal rosette; the latter, as in the flowering specimens, has externally a few scale-leaves.

The flower has five perigone-leaves densely covered with reddish-brown hairs, and five nectary-leaves[1] which are white in the first part of the flowering period, and are about twice as long as the sepals. Both the perigone-leaves and the nectary-leaves persist until the ripening of the fruits and the former become somewhat dull crimson in colour (Lindman), Norman states that the flower with ripe fruits has almost the same appearance as has the young flower. The fruit is somewhat flattened and has a rather long beak (Fig. 2).

Lindman records that the flower is protandrous in Scandinavia; my material, which was scanty in reference to this question, indicated the same. The anthers of the numerous stamens are extrorse; the filaments are short previous to flowering; the outer ones elongate first, and their anthers open after the nectary-leaves have expanded. The numerous carpels (120—150) which are closely placed in the bud do not spread out until but one or two of the numerous whorls of stamens

[1] The German "Honigblätter"; cf. Prantl.: Beitrage z. Morph. und. System. d. Ranunculaceen. Engler, Bot. Jahr., 1888.

are still in the bud-condition (Lindman). Towards the end of the flowering period the flower is homogamous, or it may be entirely pistillate (Lindman). In Central Europe *R. glacialis* is homogamous or slightly protandrous (H. Muller, Ricca). In the Alps Muller observed two flies and two small beetles visiting *R. glacialis*.

According to Kerner (l. c. pp. 162 and 276) there are three kinds of flowers in *R. glacialis*, some hermaphrodite and some pollen-bearing flowers with function-less carpels ("scheinzwittrige Pollenblüten"); the hermaphrodite are of two kinds, some with large carpels and a few small stamens, and others with small ovaries and many longer stamens; the former have cross-pollination, the latter autogamy.

Fig. 3. *R. glacialis.*

A, Nectary-leaf seen from the dorsal side; *B*, *C*, *D*, *E*, bases of nectary-leaves showing nectar-pits and the scale above with some of its variations of form. (*A*, 5/2; *B*, *C*, *D*, 5/1, from Åreskutan, 25. 7. 1884; *E*, 5/1, from Piteå Lappmark, 17. 7. 1883; Drawn by E. W.).

The nectary-leaves have upon the upper side of the claws with their yellow bases a pocket-shaped nectary. Above the latter is seated a scale (Fig. 3) which varies extremely, both in regard to form and size; even the scales from the same flower may differ greatly. The scale encloses with the nectary-leaves an angle of 40°—50° and touches the outwardly-turned ripe or open stamens with its free edges. Only an insect which can bend the stamens apart from the scales will be able to reach the honey (Kerner).

The diameter of the flower is rather variable; Norman mentions the limits of size as 2·3, and 3·1 cm. with regard to specimens from Arctic Norway; Lindman gives them as 1·5 and 2·5 cm.

The earliest flowering periods, as far as I know, are the middle of May in the Færöes (Ostenfeld, Plantevæksten paa Færoerne. Kbhv., 1906, p. 39) and the beginning and middle of June in Jan Mayen and Iceland (Herbarium-material and Dusén, Beitr. z. Fl. d. I. Jan Mayen. Bih. Kgl. Sv. Vet, Akad. Handl. Bd. 26, Afd. III, 1900, p. 5). Plants in flower have been observed on the 7th of September in Arctic Norway (Norman) and on the 16th of September, 1892, at Angmasalik in East Greenland (Herbarium-material).

As regards the dispersal of the fruit I may mention Norman's well-known hypothesis regarding its dispersal by reindeer. As far as I know it has not yet been investigated whether the dung of the reindeer contains fruits of *R. glacialis* capable of germinating; but Norman rests his hypothesis on the fact that the reindeer eat by preference the tops of this plant, even when it has ripe fruit (as has been mentioned the perianth persists) and also on the fact that the plant occurs especially in the localities in Arctic Norway in which the reindeer wander, and with a few exceptions, occurs only in those regions on the earth where that animal now lives or has lived in former times.

Germination. In the literature upon the subject there are several notes on the germinating plants of *R. glacialis*; by Lamarck in "Flore Francaise," and by L. u. A. Bravais in "Die geomet. Anordnung der Blätter und Blütenstände," Breslau, 1839, note on p. 129; and information concerning the germination may be found in several papers by Winkler in Verh. d. bot. Vereins d. Prov. Brandenburg, vols. XVIII—XXVI—XXXVI. Sylvén (l. c.) has figured and described the germinating plant from material from Lapland. Germination takes place during the spring, and there is only one cotyledon; the first leaf on the epicotyl is a scale-leaf, then comes a foliage-leaf with an entire, triangular lamina. The second year only a few foliage-leaves are developed. The third-year's leaves are distinctly tripartite; the primary root is by that time dead.

The plant grows by preference in soil poor in humus. In Arctic Norway it usually is not found below a height of 200—300 m. above tree-limit: Norman regards it also as a decidedly continental plant that is not common upon the islands. In contradistinction to this, is the fact recorded by Dusén from East Greenland, 74°—75° N. lat. that it is found there growing at shore-level and is never found at the head of fjords.

Geographical Distribution. Arctic Russia, Lapland, Finmark, Norway, Sweden, Beeren Eiland, Spitzbergen, Jan Mayen, Iceland, the Færøes, the Alps, the Pyrenees, East Greenland from 65 1/2° N. L. northwards (Lange, Dusén, see p. 342).

Anatomy. Adventitious roots of the first order. Epidermis is thin-walled, and collapsed in older roots. Exodermis is distinctly marked; the cells are somewhat radially elongated, the radial walls undulating. The epidermis and the exodermis have suberized walls, but the inner layer of the inner wall of the exodermis is of cellulose. The two outermost layers of cells of the cortex have somewhat collenchymatously thickened walls (Fig. 4). The rest of the about 15-layered cortex consists of thin-walled cells which are circular in transverse section, and of large, usually 4—5 angled, intercellular spaces. Large lysigenous lacunæ can often be seen. Next to the central cylinder there are usually a few layers of smaller and more closely-placed cells. All the cells of the cortex contained a quantity of starch (middle of July). The endodermis is slightly thickened and suberized; Caspary's dots are indistinct; the cells are somewhat tangentially elongated. Pericycle is one-layered, and the cells are isodiametric in transverse section. The vas-

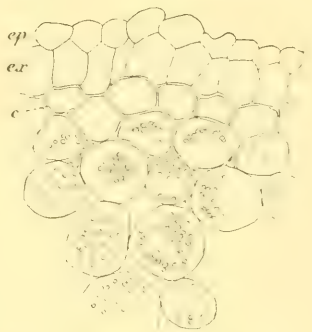

Fig. 4. *R. glacialis.* The outer layers of a root of the first order (Jan Mayen). *ep*, Epidermis; *ex*, exodermis. (215/1).

cular rays number from 3 to 5, usually 4; they may meet in the centre of the root. The sieve-tissue, as is also the case in many other species of *Ranunculus*, has in its outer part a large pentagonal sieve-tube wedged in between adjacent cells of the pericycle. Upon the inner side of the leptome-mass a few cambial divisions may be observed. The diameter of the root is from 1·5 to 2 mm. In the present species no essential differences were observed in the roots from the different localities.

The roots of the second order are very slender; 250—300 μ in diameter. The epidermis is collapsed and the exodermis well-marked. The cortex is very lacunose with about five layers of cells. Endodermis is thin-walled; the central cylinder diarch. No thickened part occurred within the exodermis. Mycorrhizas were absent; but it should be noted that in the material at hand there were only a few roots of the second order, and it is especially in the latter that mycorrhizas are found in the other species.

The rhizome. The outermost layer of the cortex together with the epidermis, is often collapsed and suberized. The cells of the cortex are elongated in a tangential direction; they contained much starch (middle of July). Hollstein records that in the interior of the cortex a continuous phellogen is developed which usually produces a layer of cork which separates off about $^1/_4$ of the cortex. I have not been able to observe anything of that kind in the rhizomes which I investigated. The vascular bundles are placed in a circle and vary in number from 5 to 10, and are of different sizes; some are circular in form, others are elongated tangentially (Fig. 5, *A*). Their course may be very irregular, usually they anastomose. Each bundle has its own endodermis, which may be slightly lignified; the cells of it also are tangentially divided; Caspary's dots are often distinct (Fig. 5, *B*). There is a cambium capable of division and the greater part of the vessels in the strands and of the wood-parenchyma is of secondary

origin (Fig. 5, *B*). The cells of the pith are arranged concentrically in relation to the vascular bundles which are near them; starch was present (middle of July).

The above-ground stem. The outer wall of the epidermis is thickened, and the cuticle is distinct; the latter is dentate in transverse section. There are a few, somewhat projecting stomata. Hairs are scanty. Within the epidermis there is a layer of cells which, in the lower part of the stem, are angular and placed closely together; higher up they are

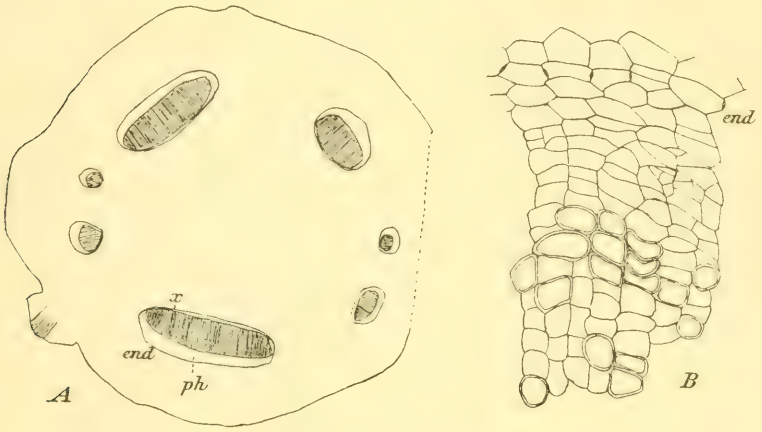

Fig. 5. *R. glacialis.*

A, Transverse section of rhizome (Tromsö; about $^{15}/_{1}$). *end*, Endodermis; *ph*, leptome; *x*, xylem. *B*, Secondary wood and sieve-tissue with endodermis; from the rhizome (about $^{260}/_{1}$).

more rounded in transverse section, and more loosely connected to the epidermis and with each other. The cortex consists of lamellæ which are one cell-layer thick and surround large lacunæ (Fig. 6, *B*). These plates are often collapsed and thereby large, irregular gaps may occur, which are largest in the lower part of the stem. The epidermis, and especially the outer part of the cortex, contains chlorophyll. The vascular bundles are placed in a circle and number from 9 to 11, and are all of about the same size; there are fewer in the peduncle than in the stem. The cells are placed closely

together around the bundles, but I did not observe any lignified stereom; on the outer side of the sieve-tissue in some of the bundles, from one to two layers of slightly collenchymatously thickened tissue can be seen. The endodermis is not distinct. Within the V-shaped mass of wood some small-celled parenchyma often occurs. Between the wood and the cambium there is in this species, as in the others, some wood-parenchyma. The cambium is but slightly developed. Interfascicular, lignified stereom is also absent, but the cells

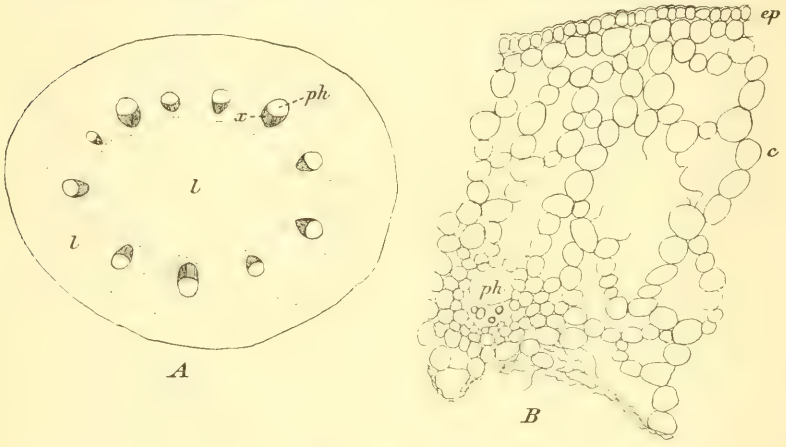

Fig. 6. *R. glacialis.*

Transverse section of stem (Jan Mayen). *A*, An entire section from near the base. *B*, Portion of section from the middle of the stem. *ep*, Epidermis; *c*, cortex; *ph*, leptome; *x*, xylem; *l*, lacuna. (*A*, about $^{20}/_{1}$; *B*, $^{75}/_{1}$).

of the medullary rays are smaller and more closely placed than are those of the cortex. The pith is more or less broken down in the stem, while in the peduncle it resembles the cortex in structure, but the lacunæ are still larger.

Such a loosely-woven stem is able to retain its erect position probably only by reason of its thickness (3—4 mm.) in combination with the pressure of the sap; and the fact mentioned above as recorded by Wydler, that the stem may lie upon the ground with its lower part prostrate, is easy to understand when reference is made to its structure.

The leaf is somewhat succulent; the upper surface is glabrous and the lower somewhat hairy with long (as much as 2 mm.), flaccid hairs. The structure of the leaf is decidedly dorsiventral; in the majority of the leaves three distinct palisade-layers (Fig. 7, *A*) were found, the height of the cells of which was about three times the breadth: the palisade-cells were slightly inclined towards the leaf-apices. There is an abrupt transition from the palisade to the spongy parenchyma which is extremely loose in structure and consists of abundantly branching cells.

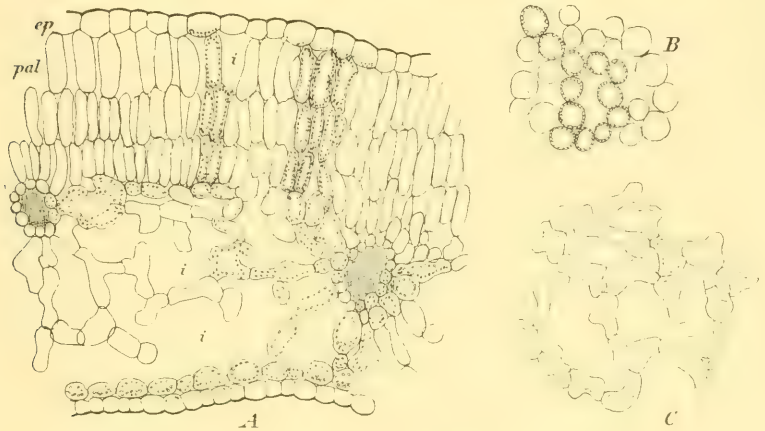

Fig. 7. *R. glacialis.*

A, Transverse section of leaf (Jan Mayen). *B*. Surface section of the uppermost layer of the palisade-tissue (Tromsö). *C*, Surface section of spongy tissue (Tromsö). *ep*. Epidermis *pal*, palisade-cells, *i*, intercellular spaces (*A*, about $^{80}/_{1}$; *B*, *C*, $^{100}/_{1}$).

The vascular bundles are surrounded by a sheath containing chlorophyll, and are entirely enclosed by the mesophyll; even above the principal vein three palisade-layers occur. The epidermis of both the upper and lower surface contains chlorophyll; the outer walls are slightly thickened. The stomata are situated on a level with the epidermis (Fig. 8, *D*). The cells of the upper epidermis have almost straight walls while those of the lower epidermis are somewhat undulating (Fig. 8, *A, B*). There are about three times as many stomata upon the upper as upon the lower surface. Th. Resvoll found 78

per sq. mm. upon the upper surface and 28 per sq. mm. upon the lower surface; my computations gave 100 and 33; in the Alpine *R. glacialis* Wagner found the numbers to be 163 and 54.

At the apex of each leaf-lobe there is a hydathode with its opening in a small depression almost at the apex of the lobe (Fig. 8, C). The cells of the epithema nearest to the tracheids are somewhat elongated and have undulating walls, towards the apex of the leaf they become shorter, but are undulating there also.

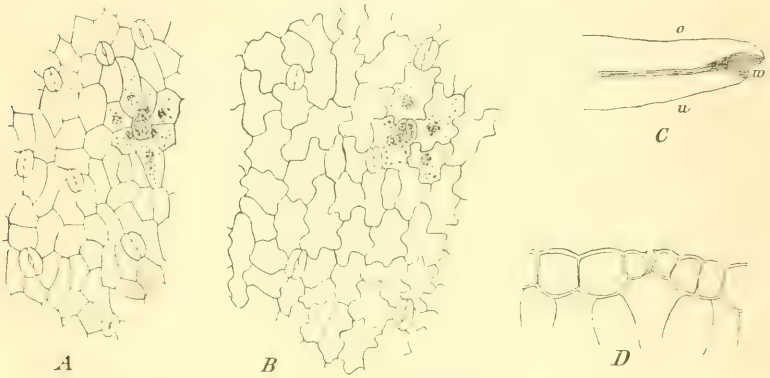

Fig. 8. *R. glacialis.*

A, Epidermis of the upper surface of the leaf (Tromsö). *B*. Epidermis of the lower surface of the leaf (Tromsö). *C*, Longitudinal section of leaf-apex, the cross-hatched part is the epithema; *o*, upper surface; *u*, lower surface; *w*, stands opposite to the hollow in which the water-pore occurs (Tromsö). *D*, Stoma from the lower surface of the leaf (Knudsho). (*A*, *B*, $^{100}/_{1}$; *C*, $^{15}/_{1}$; *D*, $^{220}/_{1}$).

In the epidermis of both the upper and lower surface sphaero-crystals of different forms occur.

The stalks of the basal leaves are almost round. The epidermis is more thin-walled than that of the stem, and contains chlorophyll. The structure of the cortex and pith is like that of those of the stem, only the lacunæ are even larger. There are about four vascular bundles without accompanying stereom. In the middle of the stalk there is a lacuna of larger or smaller size.

Ranunculus affinis R. Rr.

and

R. affinis* Wilanderi Nath.

(Syn. R. arcticus Richard., R. amoenus Led. p. p., see Simmons, 1906).

Lit. Hooker. 1833, p. 12, fig., tab. VI. Nathorst, 1883, p. 23. Borgesen, 1895, pp. 225, 236—37. Hartz, (II), 1895, p. 288. Nestler, 1895. Resvoll, 1900. Andersson & Hesselman, 1901, pp. 49—54, figs. 25—26. Dusén, 1901, p. 31. Simmons, 1906, pp. 101—08; 1909, p. 74.

Alcohol material from Spitzbergen (Middelhook in Belsund, 30. 6. 1882; Cape Thordsen, 6. 8. 1882; Gåselandet, 11. 7. 1892).

R. affinis is a perennial herb with a vertical rhizome; the latter may reach a length of as much as 5 cm., and adventitious roots arise from the whole of its surface. The rosette-leaves are long-stalked, and the laminæ somewhat reniform, always more or less deeply palmately-cleft, often into five principal lobes. I did not find scale-leaves. In most of the plants a principal bud occurred in the uppermost leaf-axil at the base of the stem, but the other leaves of the rosette may also subtend buds, and the rhizome is often found to be branched. The new shoot begins with at least two transversely-placed, long-stalked foliage-leaves; the others succeed in a $^2/_5$ spiral. The lateral shoots develop rosettes during the same year as that in which the parent-axis flowers, and when the fruit ripens some of the rosette-leaves of the parent-axis are still alive. I have noticed no instance of the principal bud flowering the same year as the parent-axis. There are 3—4 stem-leaves; the lowermost is often stalked and resembles the basal leaves, the others are sessile and pedately cleft into 5—9 oblong-linear lobes. The stem-leaves often subtend floral axes. In var. *Wilanderi*, which is altogether of lower growth than the principal form, the upper interfoliar parts of the stem in the 2—3 flowering specimens are very short so that all the floral axes appear to proceed from about the same point (Nath.). The

leaves are slightly hairy; the leaf-stalk, stem and especially the peduncle are covered with short adpressed hairs; the peduncle is furrowed.

The five perigone-leaves are hairy and somewhat violet in colour; they are outwardly or downwardly directed in the open flower and fall off early. The nectary-leaves are somewhat longer than the perigone-leaves, and are pale yellow with violet veins on the under side (Simmons, 1906); the nectary is simple and pocket-shaped (Fig. 9, *B*). The stamens are rather few in number and are situated close to the lower part of the large gynaeceum (A. & H.); the head of carpels is ovate in the young flower, but elongates somewhat and becomes cylindrical during fruit-setting: in var. *Wilanderi* it remains ovate. According to my computations the diameter of the flower was about 2—5 cm. (according to Anders. & Hesselm. it is 1·5—2 cm.) and the corolla is almost flat when it is fully expanded (A. & H.). The flowers which have been investigated from Gåselandet appear to be protogynous-homogamous. The stamens had not yet opened, nor had they elongated, but the carpels had fully-developed papillæ upon the stigmas. The plant begins to flower in the early part of July at Scoresby Sound, in East Greenland (Hartz, Dusén) and in Spitzbergen; in August it has ripe fruit (Herbarium-specimen).

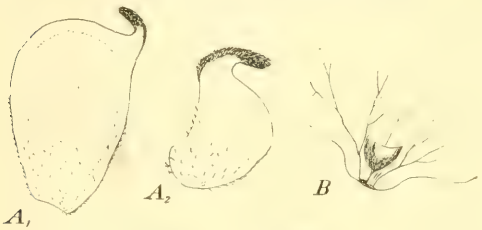

Fig. 9. *R. affinis*.

Carpels; A_1, ripe; A_2, during flowering (Cape Thordsen; $^{12}/_{1}$). *B*, Base of nectary-leaf (Spitzbergen; $^{6}/_{1}$).

Lange records that it grows in damp localities, Simmons (1906) found it in well-manured soil under a nesting-place for sea-gulls.

Geographical Distribution. West Greenland (rare), N. E. Greenland, Spitzbergen, Nova Zembla, Arctic Siberia,

Altai, Arctic America with the Archipelago, and the Rocky Mountains (Simmons, 1906).

Anatomy. The adventitious roots of the first order are triarch-tetrarch, and those of the second order diarch. Both the epidermis and the exodermis are suberized; in several specimens the former is found to have collapsed, the latter has undulating radial walls. The two outer layers of the cortex within the exodermis are slightly collenchymatously thickened; the rest of the cortex has large intercellular spaces and, in older roots, large lysigenous lacunæ. The cells of the endodermis had become slightly thickened and suberized, and several had divided tangentially. This species, as is also the case in the other species of Ranunculus which have been investigated, has a large pentagonal tube in the outer part of the sieve-tissue wedged in between adjacent cells of the pericycle. Mycorrhizas have been found, both in the principal form and in var. *Wilanderi*; it was always only roots of the second order that contained hyphæ which were often rolled together into balls.

The structure of the rhizome is similar on the whole to that of the other species with erect axes which have been investigated (Fig. 10, *A*). Stereom is absent. The epidermis and the outermost layer of the cortex are often suberized and collapsed; the cortex is lysigenously lacunose.

The cuticle upon that part of the stem which has elongated internodes, is striped. The tangential walls of the epidermis are somewhat thickened, the radial walls are furnished with pores; the epidermis contains chlorophyll. Upon the upper part of the stem the stomata are fairly numerous and they project slightly. Large intercellular spaces occur in the cortex (the sub-epidermal layer not included), but no lacunæ. The stereom, as usual, is most strongly developed in the fruit-bearing axis. The fibrous tissue outside the leptome may reach a thickness of seven layers and the lignified cells of the medullary rays

towards the circumference have somewhat thickened walls. The bundles number between 10 and 15; some wood-parenchyma occurs between the sieve-tissue and the vascular woody part from which non-lignified parenchyma was wanting, and, as was the case in several other species, some small-celled, somewhat collenchymatous parenchyma occurs on the inner side of the bundles (Fig. 10, *B*). In the peduncle there is no distinct sheath between the conducting tissue and that around it. The young flower-stalk has almost no stereom. In the older stem there is a large central lacuna.

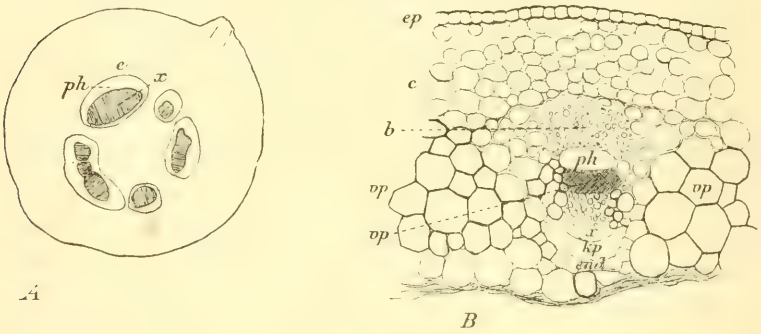

Fig. 10. *R. affinis.*

A, Transverse section of rhizome (Gåselandet; $^{17}/_{1}$). *e*, Endodermis; *ph*, leptome; *x*, xylem. *B*, Portion of transverse section of stem (Cape Thordsen; $^{90}/_{1}$). *ep*, Epidermis; *c*, cortex; *b*, bast; *ph*, leptome; *vp*, lignified parenchyma; *x*, xylem; *kp*, collenchymatous parenchyma; *end*, endodermis.

Var. *Wilanderi* was somewhat more compact in structure than was the principal form.

The thickness of the leaf varies from 210 to 250 μ, and the specimens investigated show greater differences among themselves in the structure of their leaves than is the case in any other species. The epidermis however is nearly alike in all the specimens; it contains chlorophyll, and the radial walls are more or less acutely-undulating, those of the lower surface somewhat more strongly so than are those of the upper surface (Fig. 11, *A*, *B*); the radial walls are also often perforated and are often thickened on one side in the angles; the latera!

walls of the guard-cells of the stomata often have horn-shaped thickenings which project into the lumen of the neighbouring cell like incomplete walls, (see *R. acer*, Fig. 16, *C*). The stomata are on

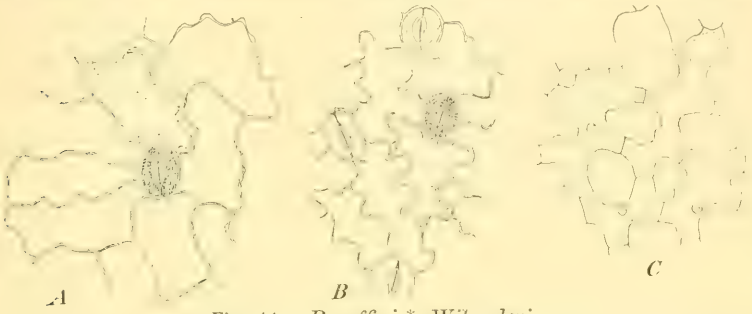

Fig. 11. *R. affinis* Wilanderi.*

A, Epidermis of the upper surface of the leaf. *B*, Epidermis of the lower surface of the leaf. *C*, Surface section of spongy parenchyma (*A*, *B* and *C*, $^{120}/_{1}$).

a level with the surface; according to Resvoll their number averages 29 per sq. mm. upon the upper surface, and 76 per sq. mm. upon the lower surface; my computation gave a similar numerical result. Nestler (l. c., p. 294) found 38 per sq. mm. upon the

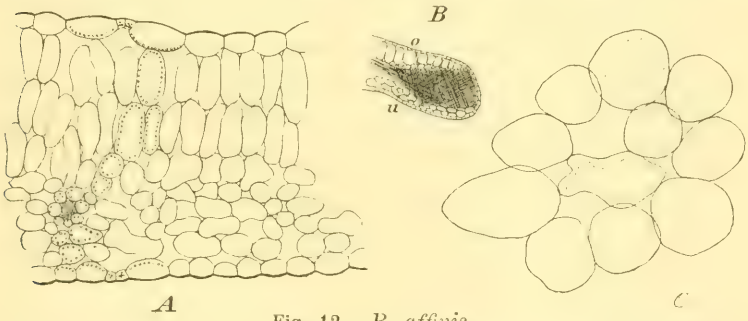

Fig. 12. *R. affinis.*

A, Transverse section of leaf (Cape Thordsen; $^{110}/_{1}$). *B*, Longitudinal section of leaf-apex (Gåselandet; $^{24}/_{1}$); tra cheids are scattered in the epithema; *o*, upper surface; *u*, lower surface. *C*, Surface section of palisade-tissue ($^{250}/_{1}$).

upper, and 69 per sq. mm. upon the lower surface. They are fairly evenly distributed, but they are absent from the larger veins where the cells of the epidermis are elongated and more or less straight-walled. The above-mentioned differences appeared in the palisade-tissue; some of the investigated specimens from Cape Thordsen (Fig. 12, *A*) had two palisade-layers con-

stituting about one-half of the mesophyll, the quota between breadth and length of the cells is $^1/_2$—$^1/_3$; the other specimens, including var. *Wilanderi* had only one palisade-layer which constituted $^1/_3$—$^1/_4$ of the mesophyll: the single palisade-cells were less regular in form than are those of the first-named specimens and their quota was on an average somewhat larger than $^1/_2$. The spongy parenchyma in these leaves was considerably looser than that in the former leaves with two palisade-layers, and consisted of more abundantly branching cells (Fig. 11, *C*).

The large bundles are accompanied by some weak stereom. Nestler (l. c., p. 301) records that he found a complete sclerenchymatous sheath; the specimens which I investigated had bast only upon the upper and under side of the bundles and in greater quantity on the lower surface. Nestler does not mention from whence his specimens originated.

Fig. 12, *B* is a somewhat diagrammatic representation of a longitudinal section through the apex of a leaf; the slanting part is the epithema in which the vessels of the bundle spread out and which opens almost at the margin. The cells of the epithema, as was the case in the other species, have strongly undulating walls.

The leaf-stalk is cordate in transverse section; its cuticle is striped and there is chlorophyll in its epidermis. Five bundles occur of which the median, outwardly-turned one is the largest. The fibrous tissue outside the leptome is fairly strong and on the sides it abuts upon the V-shaped woody parts; the endodermis is slightly lignified on the inwardly-turned part of the bundle, on the outer side it touches the fibrous tissue outside the leptome. There is a large central lacuna.

R. acer L.

Lit. Wydler, 1859, p. 267. A. Berlin, 1883, pp. 19—21. Hj. Nilsson, 1884, p. 203. Marié, 1885, p. 82. Holm, 1885, p.

41. Lindman, 1887, pp. 25, 29, 40, 42. Leist, 1889, p. 16. Schlicht, 1889, pp. 14—17, figs. 9, 10. Lubbock, 1892, p. 87, fig. 126. Rosenvinge, (I), 1892, pp. 676—77. Hartz, 1894, p. 18 Nestler, 1895, figs. 9, 18. Norman, 1895, pp. 20—23. Rosenvinge, (III), 1896, pp. 109, 127, 144, 161, 168. Ekstam, 1897, p. 147. Kerner, 1898, pp. 109, 194, 311, 699. Goffart, 1900, p. 107, figs. 340—47. Cleve, 1901, p. 51. Freidenfelt, 1904, p. 62. Sylvén, 1906, pp. 275—76.

Alcohol material from Greenland (Julianehaab, 19. 6. 1883 and Igdlorsuatsiak), Iceland (Helgavatn 7. 8. 1889), the Færöes, Denmark (several places).

The rhizome is short and vertical; it bears a rosette of long-stalked foliage-leaves with large sheaths; scales are absent. In Denmark the rosette-leaves pass the winter in a green condition (see also Sylvén), and their large sheaths densely surround the apices of the shoots. The principal bud is situated in the uppermost leaf-axil at the base of the stem; the first leaves (according to Wydler it may be the first six leaves) are often arranged in two rows: the others follow in a $^2/_5$ spiral. In Denmark it is more usual for the principal bud to flower the same year as the main axis, than it is in Greenland, Iceland and the Færöes. Other rosette-leaves may also subtend shoots. From the bases of the shoots strong adventitious roots arise, and individual shoots are fairly quickly isolated, and become independent.

The leaves of the rosette, and often the lowermost leaf upon the elongated stem, are stalked and palmately cleft into deeply-serrate or lobed segments; forma *multifidus* D. C., however, which is almost as common in Greenland as is the principal form, has the five leaf-lobes deeply tripartite with linear lobes. The upper stem-leaves are sessile.

In the leaf-axils of the elongated stems of well-developed individuals, floral branch-systems occur branching in a sympodial manner in the bracteoles, the lower branches being the most

vigorous. In Greenland the plant may attain a height of at least 53 cm. and in the Norwegian willow-bogs, as much as 176 cm. (Norman). On the other hand, individuals from exposed localities, are found which measure only 4 cm., and of which the solitary flower scarcely reaches above the rosette-leaves (f. *pumilus* Whbg.). The density of the hair-covering varies also greatly and is no doubt partly dependent upon the habitat of the plant; plants which have been growing in copses are often almost entirely glabrous, while those from exposed localities may be covered with a dense covering of white or yellowish-brown hairs (var. *Lindholmiana* Berl.).

Fig. 13. *R. acer*.

A, Base of nectary-leaf (Denmark; $^{8}/_{1}$). *B*1, Carpel from a hermaphrodite flower at time of flowering. *B*2, Carpel from a staminate flower; both from Denmark ($^{15}/_{1}$); see text.

In Greenland a form has been found with double flowers (f. *flore pleno*) in which all the stamens are petaloid (Rosenv., I); but the flower usually has five yellowish-green perigone-leaves and five nectary-leaves, glistening as if with oil; these latter have pocket-shaped nectaries the free edge of which varies greatly in form (Fig. 13, *A*). The numerous, extrorse anthers overtop the head of carpels, which is low in growth before pollination. The diameter of the flower is between 1·5 and 2·5 cm.; in Nova Zembla the diameter of that of *R. acer* f. *borealis* Trautv. is as much as 3·0 cm. (Ekstam). In Denmark the flower is eagerly visited by small beetles (*Meligethus aeneus*) and flies; Lindman found, besides several species of flies, a few *Macrolepidoptera*; Ekstam noticed flies.

In the flower-bud, the stamens overtop the carpels; but

before the flower expands the outermost stamens elongate and they open before the glistening papillæ can be observed upon the stigmas. The homogamous stage is the longer. Spontaneous self-pollination may take place at night when the flowers are closed (cf. Lindman, p. 30). In Nova Zembla Ekstam found protogynous-homogamous, homogamous, and protandrous-homogamous flowers. In Denmark I have found besides the common hermaphrodite flowers, others with carpels not fully developed; Fig. 13 B_1, B_2, shows two carpels, both from flowers of which the stamens had shed almost all their pollen; B_1 is fertile, B_2, together with the other carpels in the same flower, is without papillæ. When the flowering is over, plants are commonly found bearing, only barren, shrivelled-up carpels.

The pollen is protected from rain by the peduncle bending, during wet weather, so that the flower-cup is turned downwards.

The flowering begins in May-June, somewhat earlier in Denmark than in the Arctic regions, and may be continued into September. (Norman, Rosenvinge, II).

The fruit, like the fruits of the majority of the species of *Ranunculus*, does not appear to be especially adapted to any particular dispersal-agency. Examples of wind-dispersal are however known (Ekstam), and it may be presumed that some are dispersed by the agency of water. Of 200 fruits, which lay in quiet water, the last sunk after 3 days, while of 100 fruits, which lay in water which was frequently stirred, all sank before the expiration of 24 hours. Norman believes that synzoic dispersal by means of cattle takes place, and mentions having found germinating plants in cow-dung. I fed a heifer, in May, 1910, with fruits of the previous year, and 36 hours after, 80 apparently unhurt specimens of these were washed out of the dung; they were immediately sown and seven (8·8 %) germinated.

Sylvén is of opinion that *R. acer* usually germinates in spring, but under cultivation the fruits will germinate immediately after maturation, and in Denmark I have observed young germinating plants in August. In the plants which germinate in spring the primary root of the seedling and also the hypocotyl live only the first summer, and adventitious roots are developed early from the base of the epicotyl. The sheaths of the cotyledons are slightly coherent (Sylvén, Lubbock, 1892).

In Arctic Norway the frequency of occurrence of this species is similar from sea-level to high up in the mountains, with local accumulations in the cultivated home-fields and on the snow-line; in the latter place it often occurs as f. *pumilus*, (Norman). In Iceland also it is common in cultivated meadows, a fact which is perhaps to be connected with its above-mentioned dispersal by cattle. In South Greenland it is common on grass-land, grassy slopes and in willow-copses in the exterior of the country (Rosenv., III). In northern Sweden it grows on damp ground (Cleve), and in Nova Zembla it occurs on the tundra on dry, stony ground (f. *borealis* Trautv.) (Holm).

Geographical Distribution. Arctic America, Greenland, Iceland, the Færöes, northern and central Europe, the Alps, Caucasus, Arctic Russia, the Urals, north-east Siberia and Nova Zembla.

Anatomy. In the roots of the first order the outer walls of the epidermis are somewhat thickened, the exodermis is distinctly marked, the cells are radially elongated and the radial walls undulating. Both the epidermis and exodermis are suberized. The cortex is 15—17 layers thick and contains starch; the starch-grains are compound. The two subexodermal layers of the cortex are somewhat collenchymatously thickened, the others are thin-walled and collapse more or less according as to whether the plant grows in damp or in dry ground. (Freidenfelt). The endodermis of the mature root is thickened and lignified, with thin-walled passage-cells opposite

to the 4—5 radial masses of wood of the central cylinder. According to Freidenfelt the cambium can develop in older roots some secondary wood. The leptome-mass has the usual large pentagonal tube which is wedged in between adjacent cells of the pericycle.

The roots of the second order have an exodermis and endodermis like those mentioned above; all the layers of the cortex (about 4) are thin-walled, also the endodermis, which is corky. The central cylinder is diarch. Schlicht has found endotrophic mycorrhizas in the lower part of the primary root and in roots of the second order. The specimens from Denmark, the Færöes and Iceland which I investigated also had mycorrhizas in the above-mentioned parts of the roots. The hyphæ were often rolled together into compact balls in the inner layers of the cortex. Roots from Greenland have not been investigated.

The rhizome. (Compare Hj. Nilsson). In the specimens investigated, the epidermis was, for the most part, collapsed, together with the outer layer of the cortex, and was corky like the latter. The slightly irrregular cells of the cortex were somewhat tangentially elongated; the outermost living cells had rather thick walls. The bundles were often grouped irregularly around the pith; they anastomosed, and in the thicker rhizomes they were not placed in any one circle. The Danish specimens had a few-layered fibrous tissue outside the leptome and a sheath of strong wood-parenchyma on the inner side of the woody part. The Færöese specimen which has been investigated also had this inner arch of stereom, but in the Iceland specimens all lignified stereom was wanting. The endodermis was fairly distinct, and was lignified; it had tangentially elongated cells. The cells of the pith were irregular; in an old, Danish specimen there were many scattered sclerenchyma-cells in the pith. The cortex and the pith contained starch. Rhizomes from Greenland have not been investigated.

What has been said above with regard to the rhizome applies also to the structure of the stems, viz. that the specimens from Iceland which have been investigated have a smaller amount of lignified stereom than those from Denmark. The Greenland specimens were similar on the whole to those from Iceland. The epidermis also was stronger in the Danish specimens (outer walls about 6 μ thick) than in the others. The cuticle was striped; the stomata were situated on a level with the surface. The Greenland and Iceland specimens had much

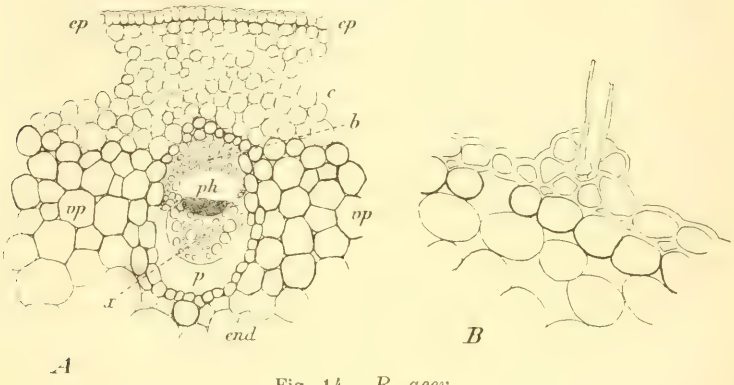

Fig. 14. *R. acer.*

A, Portion of transverse section of stem (Greenland; about $^{80}/_{1}$). *p*, Non-lignified parenchyma; between leptome and xylem there is some wood-parenchyma; the letters as in Fig. 10, *B*. *B*, Base of hair with the epidermis and the outermost layer of cortex of peduncle (Greenland; $^{250}/_{1}$).

chlorophyll in the epidermis, the Danish had none at all or but little.

Of the 6—10 layers of the cortex the outer are richer in large intercellular spaces than are the inner; but none are present between the epidermis and the subepidermal layer. The bundles (Fig. 14, *A*) range in number from ten to many and are unequal in size. In the Danish specimens the fibrous tissue outside the leptome attains a thickness of as many as nine layers and is very strong; the thickness of the interfascicular lignified parenchyma is as great as six layers and it has, in some parts, somewhat thickened walls. A few layers of somewhat

thickened and often also lignified parenchyma including the endodermis formed the stereom on the inner side of the strand; the endodermis on the outer side of the fibrous tissue outside the leptome is much thickened and lignified. Between the rudimentary cambium and the vessels which lie scattered in the wood-parenchyma there occurs a mass of wood-paren-

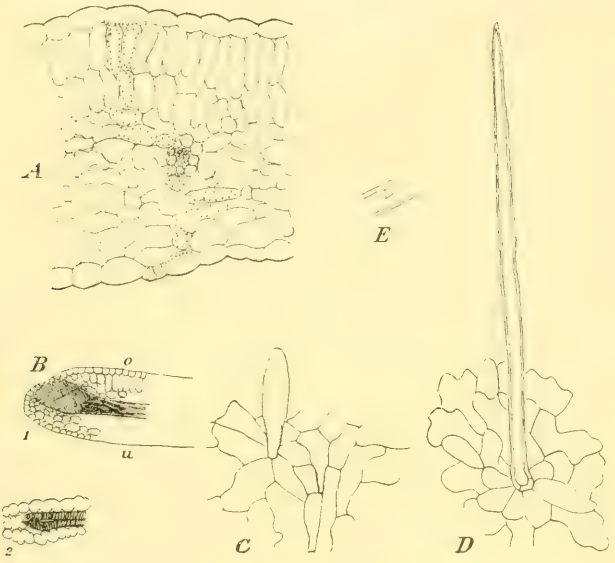

Fig. 15. *R. acer.*

A, Transverse section of leaf (Greenland; $^{100}/_{1}$). *B*, *1*, Longitudinal section through leaf-apex with epithema (cross-hatched). *o*, Upper surface; *u*, lowers urface ($^{25}/_{1}$). *2*, Tracheids with epithema-cells (Greenland; $^{120}/_{1}$). *C*, Club-shaped hair from the upper surface of the leaf. *D*, Small ordinary form of hair from leaf (Denmark; $^{85}/_{1}$). *E*, Octahedral crystal lying in a hair from leaf (Denmark; $^{220}/_{1}$).

chyma; and between the vessels and the endodermis, a larger or smaller portion of non-lignified parenchyma is found. Lignified stereom is quite absent from the young peduncle and not until after flowering does it develop. The pith is almost entirely broken down quite early. The hairs are unicellular, fairly thick-walled and slightly lignified.

The Greenland and Iceland specimens, with the exception of the above mentioned modifications, resemble those from Denmark.

The thickness of the leaf in Danish and Greenland specimens was 300—340 μ, in those from Iceland 160—225 μ.

Two kinds of hairs occur upon the leaves; the more common (Fig. 15, *D*) are like those of the stem, and some of them contain crystals of a substance, of which the base is calcium-hydrate; the others (Fig. 15, *C*) only occur along the veins of the upper side and are club-shaped, thin-walled, and rich in contents (compare Nestler, p. 291, Fig. 18).

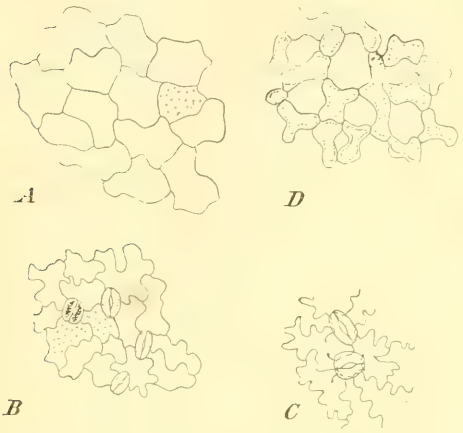

Fig. 16. *R. acer.*

A, Epidermis of the upper surface of the leaf (Iceland). *B*, Epidermis of the lower surface of the leaf (Iceland). *C*, Epidermis of the lower surface of the leaf (Denmark). *D*, Surface section of spongy parenchyma of leaf from Greenland, (A, B, C and D $^{300}/_{1}$).

The epidermis of the leaves from northern localities, but Denmark can scarcely be included, contains chlorophyll; otherwise it is nearly alike in the Danish and Icelandic specimens. In the latter the radial walls of the cells of the upper surface are less undulating than those of the lower surface, which has strongly undulating walls especially in the Danish specimens. In these latter incomplete walls often proceed from the radial walls, especially from the guard-cells of the stomata (cf. *R. affinis*; and see Fig. 16, *C*); there are found only mere indications of such a condition in the leaves from other localities. In the Greenland specimens the radial walls of the epidermis of the lower surface are almost similar to those of the upper surface in the Iceland specimens, while those of the upper surface are slightly curved. The stomata are situated on a level with the surface, are fairly evenly distributed and their

longitudinal axes have no fixed direction. Nestler found 15 stomata per sq. mm. upon the upper surface and 98 per sq. mm. upon the lower surface (l. c. p. 294); he does not give localities for his specimens. The specimens from Denmark, Iceland and Greenland which have been investigated have per sq. mm. upon the upper and lower surface, from 0 to about 85, from 0 to about 90, and from about 30 to about 150, respectively. There is great variability in the number of the stomata in the leaves from Iceland and also in those from Greenland.

The Danish and Icelandic specimens have one palisade-layer those from Greenland have generally two layers (Fig. 15, *A*); everywhere the palisade-layers constitute from $^1/_3$ to $^1/_2$ of the thickness of the mesophyll, and the quota of the individual cell is generally from $^1/_3$ to $^1/_2$. The spongy parenchyma in the upper part is distinctly more compact than in the lower, and in the Danish and Icelandic specimens it consists of longer and more abundantly branching cells than in those from Greenland (Fig. 16, *D*).

Upon the upper surface the lamina is depressed like a gutter over the larger veins, and the latter are accompanied upon the upper and lower surface by stereom, which reaches to the epidermis. The smaller veins are surrounded only by a sheath which contains chlorophyll.

At the leaf-apices there is an epithema the pores of which open upon an oblique plane. The cells are often branched in several planes and the walls are undulating, as in *R. nivalis* (Fig. 15, *B*).

The leaf-stalk is cordate in transverse section. The bundles number 5—15, alternately large and small; in structure they are similar to those of the stem from the same place, but no inner arch of stereom occurs. Interfascicular stereom is absent. The structure of the cortex and epidermis is similar to that of those of the stem. The epidermis contains chlorophyll. The pith is broken down gradually.

Ranunculus sulphureus Sol.

Syn. *R. altaicus Laxm.*

Lit. Hartz, (II), 1895, p. 288; (III), 1895, p. 332. Norman, 1895, p. 17. Ekstam, 1897, p. 147; 1899, p. 23. Abromeit, 1899, p. 31. Th. Resvoll, 1900, fig. 3. Andersson & Hesselman, 1901, p. 19. Dusén, 1901, p. 30. Simmons, 1906, p. 108; 1909, p. 74.

Alcohol material from Greenland (Scoresby Sound, 18. 7. 1892); Norway (Lyngen, 7. 8. 1884); Spitzbergen (Hornesund, 25. 6. 1882, Belsund, 1. 7. 1882, Rendalen in Sassenbay, 15. 7. 1882, Tampetberg, 17. 7. 1882, King Charles Land, 4. 8. 1898, Advent Bay, 8. 8. 1910); Nova Zembla.

Malmgren (Spetsb. Fan. Fl. K. Sv. Vet. Akad. Översigt, 1862) writes that *R. altaicus* has longer styles than *R. sulphureus* and that its nectary-leaves are obcordate (quoted in Simmons, 1906, p. 108). Simmons finds no reason to consider these two as distinct species, as the characters mentioned are not constant; he will go no further than to call *R. altaicus* a variety of *R. sulphureus.* One of the individuals in the material from Scoresby Sound had nectary-leaves some of which were slightly emarginate at the apex and the others rounded. As far as I have been able to see, there is no difference in the anatomy of the two forms.

The rhizome is either slanting or vertical and may live several years. The longest which I measured had a length of about 3 cm. The adventitious roots arise especially from the nodes (Fig. 17). Rhizomes are often found with rather numerous ascending branches. Each such branch bears a rosette consisting only of foliage-leaves, in number rarely exceeding five; very often there is but one or two. In flowering specimens the rhizome is continued into a stem with elongated internodes which bears as many as four foliage-leaves; the lowermost of these is stalked, the upper are sessile. The arrangement of the leaves is $^2/_5$, with the exception of the first

two leaves of the shoot which are probably transversely-placed. Usually only the main axis flowers, but the stem-leaves may subtend floral axes; these axes bear from one to two green bracts. The stalked stem-leaf probably rarely subtends flowers, but upon vigorous specimens a shoot is fairly frequently developed in this axil, which however can scarcely produce more than two transversely-placed, stalked foliage-leaves. The principal bud is situated in the uppermost leaf-axil at the base of the stem (Fig. 17); frequently the leaf below also subtends a bud. Consequently, the shoot almost resembles in appearance that of *R. glacialis,* only, in *R. sulphureus,* the scale-leaves are absent. The plant probably passes the winter as does *R. nivalis* (see figure in Kjellman l. c., p. 493): the sheaths of the fully-developed leaves of the rosette surrounded the shoots of the next year, the leaves and terminal flowers of which are formed even during autumn.

Fig. 17. *R. sulphureus.*
(Scoresby Sound; 18. 7. 1892; 3/4).
I, Main axis; II, the two-leaved principal bud; *b*, the subtending leaf.

The height of the flowering plant is usually from 6 to

16 cm. (Norman l. c.). I have measured herbarium specimens from Nordfjord in Disco which were about 35 cm. in length. A dwarf specimen is shown in Fig. 18.

Fig. 18. *R. sulphureus.* (King Charles Land).
Dwarf-plant which had been growing on sand near the shore.

There are five reddish-brown, hairy perigone-leaves and five yellow nectary-leaves about twice as long as the perigone-leaves. The receptacle is almost globular in form but elongates somewhat during fruit-setting, not so much, however, as in *R. nivalis*. These two plants, *R. sulphureus* and *R. nivalis* agree very closely but are distinguished from each other especially by the fact of *R. sulph.* having short, reddish-brown hairs upon the torus, while they are absent from *R. nivalis* (Simmons l. c.). The nectary occurs upon the claw of the nectary-leaf (Fig. 19) and consists of a simple pocket. Ekstam (1899, l. c.) records that in Spitzbergen the flowers have a slight perfume, and that they are proterogynous-homogamous; but self-pollination is rendered difficult by the fact of the gynoecium overtopping the stamens considerably even when the latter have opened. The anthers are partially extrorse. In Arctic Siberia and in Nova Zembla the diameter of the flower is about 16 mm. (Ekstam, 1897); in Scandinavia the maximum is

Fig. 19. *R. sulphureus.*
A, Base of nectary-leaf with nectary (7/1). *B*, Almost ripe fruit; about 7/1 (Spitzbergen; S. S. 1910).

30 mm. (Ekstam, 1897). Several species of flies have been noticed upon the flowers in Spitzbergen (Ekstam). In the middle of June the plant appears to be in full flower everywhere and ripe fruit is found at the middle and end of August (Andersson & Hesselman; Ekstam), but the flowering period may continue as long as into September (Sept. 9; Norman l. c.). Fruit is set abundantly.

The nuts are smooth and somewhat flattened, and the beaks are rather long (Fig. 19); they are dispersed by the agency of the wind (Ekstam 1897).

According to Norman, in Arctic Norway this species is not so particular in its requirements regarding habitat as *R. glacialis*; it occurs both at the shore and in the interior of the country; in the lowlands and in the highlands (willow-zone). In N.E. Greenland it is no doubt most frequent in the coastal districts (Dusén l. c.). In Arctic Norway it appears to grow by preference in rather damp ground or in gravel, and is also found in marshy localities. Hartz found it growing in a bog in Scoresby Sound.

The species is circumpolar but does not occur exclusively in Arctic regions as it is also found in North America in the Rocky Mountains, and in Asia it extends towards the south as far as to the Baikal-Mountain regions and to Altai. In Europe it occurs only in Finmark (Simmons l. c.).

Anatomy. I am not prepared to say anything regarding the main root; it probably dies early as is commonly the case in the genus *Ranunculus*; the adult plant bears only adventitious roots. The anatomy of the latter does not differ in any essential points from the root-structure described for *R. glacialis*, which may very well be regarded as a type, at least as far as the Arctic species of *Ranunculus* are concerned.

The epidermis in the adventitious roots of the first order has perhaps less tendency to collapse and the exodermis is not so distinct as in *R. glacialis*; both the layers are

suberized. A somewhat thickened, subexodermal layer occurs and the cortex has larger or smaller lacunæ. The endodermis is somewhat thickened and the central cylinder is diarch to tetrarch.

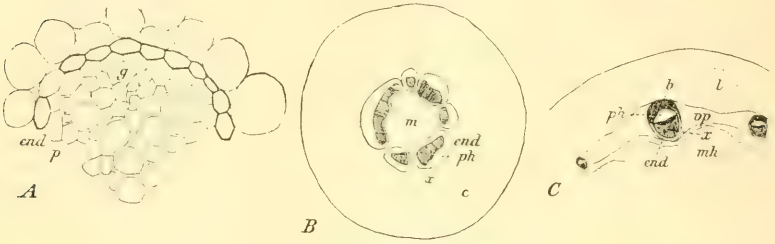

Fig. 20. *R. sulphureus.*

A, Portion of section of central cylinder of adventitious root of the first order (Scoresby, Sound; $^{165}/_{1}$). *B*. Transverse section of rhizome (Spitzbergen; $^{8}/_{1}$). *C*, Portion of transverse section of stem (Spitzbergen; about $^{20}/_{1}$); *b*, bast; *c*, cortex; *end*, endodermis; *g* the large pentagonal sieve-tube; *l*, lacuna; *m*, pith; *mh*, pith-cavity; *p*, pericycle; *ph*, leptome; *vp*, lignified parenchyma; *x*, xylem.

There is a large sieve-tube on the outside of each group; cambium is absent (Fig. 20, *A*).

The root of the second order consists of epidermis, about five layers of cortical cells and a diarch central cylinder. The epidermis as well as large parts of the cortex are collapsed; a thickened subexodermal layer does not occur. The epidermis and the indistinct exodermis are suberized. Here also a large sieve-tube occurs on the outside of each group of sieve-tissue.

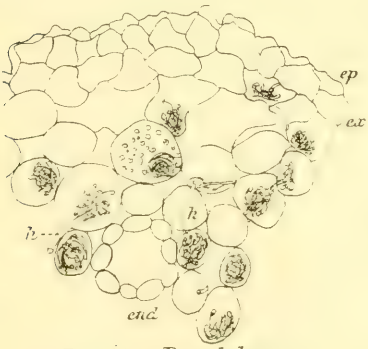

Fig. 21. *R. sulphureus.*

Portion of transverse section of root of the second order showing mycorrhizas (Nova Zembla; $^{220}/_{1}$); *ep*, epidermis; *ex*, exodermis; *end*, endodermis; *h*, hyphæ.

Mycorrhizas have been found in specimens from all the habitats and the hyphæ often occur in large quantities in the lower, slender parts of the roots of the first order and in the roots of the second order. Balls of hyphæ, whenever such occur, are most frequently found in the inner cells of the cortex (Fig. 21).

The starch-grains are compound.

The rhizome (Fig. 20, *B*), also, resembles in the essentials of its structure that of *R. glacialis*. The outer walls of the cells of the epidermis are somewhat thickened, but often the epidermis is dead, in which case the cells lying within become somewhat collenchymatously thickened; often the outer layers of the latter also die. The cortex contains abundance of starch (June), the grains are compound; the cortical cells are slightly tangentially elongated, and there are fairly large intercellular spaces, I have not been able to find any phellogen in the rhizome either in this species or in any of the other in my material; as mentioned on p. 344 Hollstein notes that it occurs in *R. glacialis*. The vascular bundles vary in number, and are arranged in a circle, each of them surrounded by an endodermis with Caspary's dots. They often anatomose, which causes the form, size and number to vary in different sections of the same rhizome. The cambium is capable of division, and the greater part of the wood (vessels + parenchyma) and the sieve-tissue is of secondary formation. The endodermis is often somewhat lignified. The pith is like that in *R. glacialis*.

The Stem is stiffly erect in contradistinction to *R. nivalis* in which the stem bends sideways (Simmons); it is rounded and thinly covered with hairs; the flower-stalk is more hairy than the stem. In herbarium-specimens the lower part of the stems of the preceding year are often found to arise from the rhizome below the rosette.

The structure is essentially like that of the stem of *R. nivalis*. The cuticle is grooved and the epidermis which contains chlorophyll has fairly thick tangential walls. The stomata are on a level with the surface. The cortical tissue is often found to be dead in scattered patches. A great part of the pith in the flowering stem is broken down, leaving a large hollow space in the centre. The vascular bundles (Fig. 20, *C*)

occur in numbers varying from 10 to 15 and are of different sizes, large and small alternating almost regularly; upon their outer side there is fibrous tissue, from 3 to 5 layers thick, consisting of lignified cells with thick walls. This layer of tissue abuts directly upon the sieve-tissue and is continued to the sides as an interfascicular portion of lignified parenchyma forming a boundary between the pith and the cortex. This strengthening-ring (A. Meier's "Festigungsring") consists of from 2 to 4 layers of cells, the walls of which are slightly, or else not at all, thickened. Around each vascular bundle is a lignified endodermis, which is most easily seen upon the inner side of the bundle; externally its cells resemble those of the fibrous tissue. Between the cambium and the vessels there is some wood-parenchyma, and between the vessels and the endodermis non-lignified parenchyma occurs.

The flower-stalk is slightly furrowed and is more densely hairy than the stem. The hairs are unicellular and rather long. The vascular bundles are fewer in number than in the stem, and during flowering, stereom is almost absent, but it develops afterwards during fruit-setting and becomes stronger than that in the stem. The outermost part of the cortex has larger intercellular spaces than has the inner. There was no special endodermis around each single vascular bundle and a common one was not distinct in the specimens examined.

The stem contains but a small amount of starch (middle of July), the grains are compound.

The Leaf. The rosette-leaves and often the lowermost stem-leaf are stalked; in form they are short and broadly ovate and often with a somewhat wedge-shaped base; the margin is divided into a varying number of shallow, short, broad lobes. The sessile stem-leaves are more or less deeply 5—7 lobed. Hairs occur along the margin, but otherwise the leaves are glabrous. No difference has been found between the anatomy

of the basal leaves and that of the stem-leaves. The outer walls of the epidermal cells are slightly thickened; the radial walls are somewhat undulating and almost alike in the epidermis of both surfaces (Fig. 22, *C*, *D*); but above the larger bundles

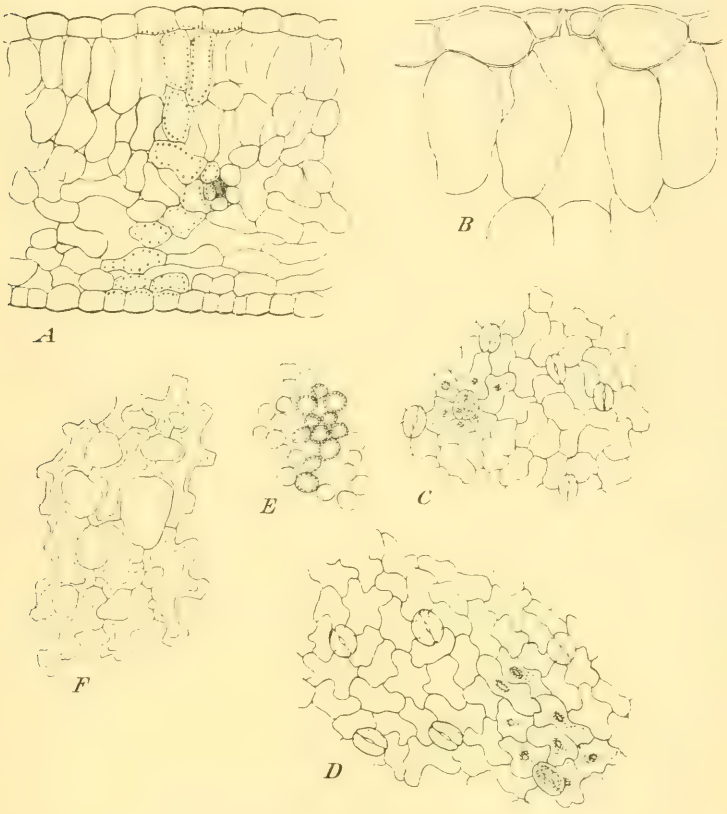

Fig. 22. *R. sulphureus.*

A, Transverse section of leaf (Scoresby Sound). *B*, Stoma from the upper surface of the leaf. *C*, Epidermis of the upper surface of the leaf. *D*, Epidermis of the lower surface of the leaf. *E*, Surface section of uppermost palisade-layer. *F*, Surface section of spongy parenchyma (*B*, *C*, *D*, *E*, *F* are from Spitzbergen; *A*, *C*, *D*, *E*, *F*, $^{160}/_{1}$; *B*, $^{250}/_{1}$).

the epidermal cells are nearly straight-walled and are elongated parallel with the bundles. The epidermis contains chlorophyll, and sphæro-crystals are found in many cells. The stomata are either on a level with the surface or project slightly, and here

as in other species of *Ranunculus* the outer, lateral walls of the guard-cells in transverse section are convergent inwards (Fig. 22, *B*). In the lobes the stomata are arranged more or less parallel with the main bundle, otherwise they are without any fixed order. According to my computation about the same number of stomata occur per sq. mm. upon both surfaces of the leaf, viz. about 70. Th. Resvoll found 67 per sq. mm. upon the upper and 83 per sq. mm. upon the lower surface. Th. Resvoll records 2—3 palisade-layers. The leaves I investigated had two layers which taken collectively constituted $^1/_2$—$^1/_3$ of the thickness of the mesophyll. The individual cells of the palisade-layers are usually barrel-shaped; the uppermost layer is often higher than the lower ones, and in some places the palisade may be said to occur in but one layer, the cells of which are then more strongly differentiated as palisade-cells. The palisade-cells are slightly inclined towards the leaf-apex. Usually there is a rather distinct passage from the palisade to the spongy parenchyma; the latter is very lacunose in structure and is composed of branched, often somewhat stellate cells (Fig. 22, *F*). Long slit-like lacunæ often occur within the subepidermal layer upon the lower surface.

Along the main bundles of the leaf, upon both the upper and lower surface, run elongated elements which in transverse section are circular, close-set, and non-prosenchymatous; they touch the epidermis of both surfaces; along the somewhat weaker bundles such cells occur only upon the lower surface, while the palisade-layers upon the upper surface are not invaded; the smaller bundles are surrounded only by a sheath containing chlorophyll (Fig. 22, *A*). Here as in other species, each lobe terminates in a hydathode in which the mesophyll is transformed into an epithema the intercellular spaces of which open out in water-pores, in exactly the same manner as in *R. nivalis* (see Fig. 27, *A*).

The dwarf-plant from King Charles Land (Fig. 18) had leaves

which were somewhat looser in structure than were those in the other specimens which were investigated. It was found growing upon a sandy shore and had a very vigorously developed root-system.

The leaf-stalk is reniform in transverse section. There are three vascular bundles and they are certainly not accompanied by stereom; the endodermis is only slightly evident. The pith has a tendency to collapse so that a larger or smaller lacuna is formed. The cortex nearly resembles that of the stem in structure. The epidermis contains chlorophyll; it, also, resembles that of the stem.

No differences have been found in the structure of the individuals investigated from the different localities, with the exception of the dwarf-plant from King Charles Land.

Ranunculus nivalis L.

Lit.: Buchenau & Focke, 1872, p. 28. Kjellman, 1883, p. 493. Holm, 1885, p. 50, tab. XI, figs. 6—7. Lindman, 1887, p. 42, tab. I, fig. 10. Borgesen, 1895, pp. 225, 231, 236, fig. 48, resumé: Journal de bot., IX, 1895. Hartz, II, 1895, p. 288; III, 1895, p. 331. Norman, 1895, p. 14. Ekstam, 1897, p. 146. Abromeit, 1899, p. 30. Ekstam, 1899, p. 23. Andersson & Hesselman, 1900, p. 48. Resvoll, 1900, figs. 2, 8, 9, 12, 31. Cleve, 1901, pp. 51, 103. Dusén, 1901, p. 30. Freidenfelt, 1904, p. 53. Simmons, 1906, p. 110. Sylvén, 1906, p. 274, tab., XXV, fig. 2.

Alcohol material from Disco in Greenland, 20. 7. 1884; Kaafjord in northern Norway, 16. 7. 1885; Spitzbergen, 6. 8. 1910.

The rhizome is either vertical or oblique and may attain a length of as much as 5 cm. The primary root dies early, but adventitious roots arise especially from the nodes of the rhizome; a sympodium is formed when flowering begins. The stem is erect and ribbed, especially the fruit-stalk, and it is hairy with reddish-brown hairs which are most dense upon the peduncle. Some dwarf individuals from Hudson Strait which I measured were 2 cm. high, but the usual height is

8—10 cm. at the beginning of the flowering period and 15—25 cm. towards the time for the ripening of the fruit. The stem is, at that time, not rigidly erect as in *Ran. sulphureus* but "spreads then outwards, and becomes assurgent" (Simmons l. c.). The full-grown plant bears only foliage-leaves (Kjellman l. c.), but before it attains the flowering stage, according to Sylvén (l. c.) it has developed even in October a winter-bud protected by scale-leaves. The rosette-leaves are usually few in number, and long-stalked; they are cordate at the base and are deeply three-cleft. There are 2—3 stem-leaves; the lower one is stalked and is similar in form to the rosette-leaves, the others are sessile and simpler in form (Fig. 23). The principal bud occurs in the axil of the uppermost basal leaf, but the other leaves of the rosette may also subtend buds and the rhizome is often found to be branched. The two lowermost stem-leaves may subtend floral-axes which are usually much more slender than the main axis; they bear one or two green bracts. In the specimens from Spitzbergen (leg. 6. 8. 1910) the principal bud had an almost fully-developed flower, with fully-developed hairy perigone-leaves and nectary-leaves and far advanced stamens and carpels. The young stem-leaves

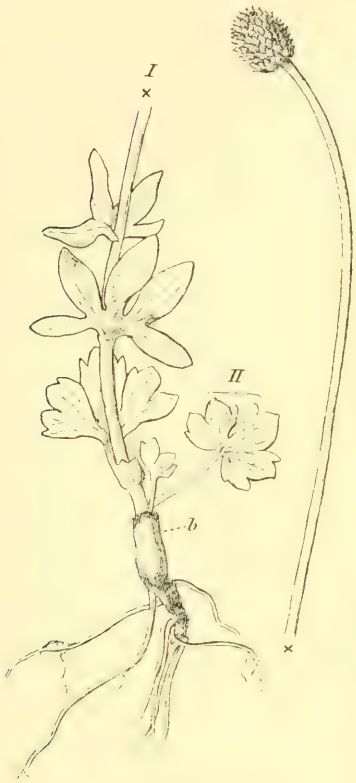

Fig. 23. *R. nivalis.*
(Advent Bay in Spitzbergen; 6. 8. 1910; 5/6). *I.* Main axis; *II.* principal bud subtended by *b* which is the dead sheath of the uppermost rosette-leaf upon axis I.

surrounded the flower and apparently formed its chief protection; there were, in addition, two unexpanded basal foliage-leaves with large sheaths, and below two fully-developed leaves, the thin, translucent sheaths of which encompassed the bud. The leaves of the parent-axis had withered (cf. KJELLMAN, l. c. Fig.). The other buds of the rosette may attain the flowering stage in the same year as the principal bud; but probably, as a rule, this is delayed until they have become stronger. The dead flower-axes often persist on the rhizome throughout the winter.

The flower has five perigone-leaves which are densely covered with reddish-brown hairs and are half the length of the oval nectary-leaves; they are bright yellow in colour. The cluster of fruits is oblong; it grows considerably in length after fertilization and becomes as much as 14 mm. high. The fruits are somewhat flattened and have a rather long and straight beak (Fig. 24, *B*). The nectary-leaves have at their base an open pocket-shaped nectary (Fig. 24, *A*). The flower differs in structure from such as that of *R. acer*, in which the flower is flat and the stamens longer than the carpels; in the present species the flower is deep and narrow, the stamens short and the head of carpels is high and convex (LINDMAN l. c. Tab. I, Fig. 10). In Spitzbergen the diameter of the flower is 10—12 mm. (EKSTAM) and in Greenland 15—23 mm. (WARMING, notebook). Both LINDMAN and EKSTAM record that it is proterogynous-homogamous, and the latter thinks that self-pollination cannot easily take place, as the pistil and stigma grow considerably after pollination. In Spitzbergen the flower has a slight perfume, it is visited by

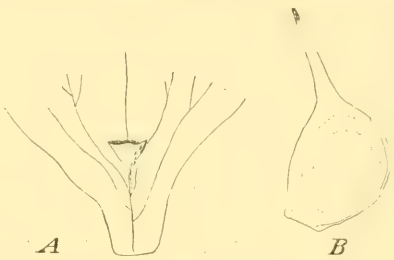

Fig. 24. *R. nivalis*.
A, Base of nectary-leaf with nectary (Kaafjord; $^8/_1$).
B, Almost ripe fruit (Spitzbergen; 6. 8 1910; $^5/_1$).

Diptera (Ekstam). Lindman has proved by experiment that it sets ripe fruit after self-pollination. The flowering begins in the middle of June, and the fruit ripens in August. Ekstam (1897) did not find ripe fruit in Nova Zembla, but records such from Arctic Siberia. He states that the fruit is dispersed by the agency of the wind. Norman thinks that reindeer are concerned in Arctic Norway with the dispersal of the fruit.

According to A. Cleve (l. c.) *R. nivalis* germinates during autumn (December), but seeds which had been sown by Sylvén in flower-pots germinated during the following spring. In the first stages of its development *R. nivalis* resembles *R. pygmæus*, but is distinguished from the latter by less decided heterophylly. The two cotyledons are long-stalked, the lamina is oval-lanceolate, and the sheaths are coherent at their base. The primordial leaf is tripartitely lobed in front (Sylvén).

During the first weeks of the period of vegetation in spring, *R. nivalis* appears to require a cold soil, wetted by melting snow, but afterwards the soil may become dry without injury (Cleve, Norman). In Spitzbergen the plant grows both upon grassy slopes and also in marshy ground, and at Scoresby Sound in East Greenland in damp clay. In Norway it is a markedly continental plant that may extend very high up into the mountains (1550 m. above sea-level); in East Greenland it is not very probable that it will be found at the heads of the of the fjords (Norman, Hartz, Dusén).

Geographical Distribution. (Holm). Arctic America, Greenland, Spitzbergen, Scandinavia, Arctic Russia, Nova Zembla, North Siberia.

Anatomy. The structure of the root (Fig. 25, *A*, *B*) was similar in specimens investigated from all the regions from which I had material, and did not differ in any essential points from that of the root of *R. glacialis*. The epidermis has a tendency to collapse, both it and the exodermis are suberized. From one to two of the outermost layers of the

cortex are collenchymatously thickened, but only in roots of the first order. The cortex acquires at an early stage large, lysigenous lacunæ. The endodermis is suberized, but the walls are not thickened. The central cylinder is di- or triarch in roots of the first order and diarch in roots of the second order. The latter contain hyphæ which are usually found rolled together into balls in the inner layers of the cortex Fig. 25, *C*); such mycorrhizas have been found in specimens from Disco, Kaafjord and Spitzbergen.

The rhizome is similar to that of *R. glacialis.*

The stem above ground nearly resembles in structure

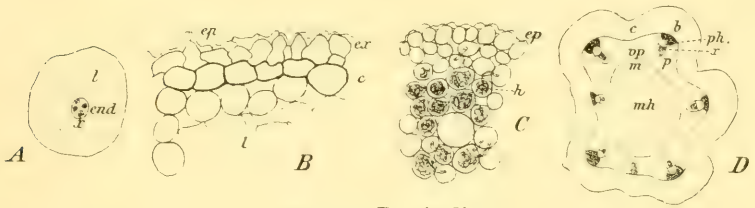

Fig. 25. *R. nivalis.*

A, Transverse section of adventitious root of the first order (Disco; about $^{20}/_{1}$). *B*, Portion of A (about $^{110}/_{1}$). *C*, Mycorrhiza of root of the second order (Kaafjord; $^{60}/_{1}$). *D*, Transverse section of peduncle (Spitzbergen; 6, 8. 1910; about $^{18}/_{1}$). *b*, Bast; *c*, cortex; *end*, endodermis; *ep*, epidermis; *ex*, exodermis; *h*, hyphæ; *l*, lacuna; *m*, pith; *mh*, pith-cavity; *p*, non-lignified parenchyma; *ph*, leptome; *vp*, lignified parenchyma; *x*, xylem.

that of *R. sulphureus*. The cuticle is more slightly striped than in the latter. The stomata are on a level with the surface. The epidermis contains chlorophyll and is attached to the outermost layer of the cortex; the rest of the lacunose cortex, extending inwards to the ring of stereom, is about five layers thick. The development of the stereom is about equal to that in *R. sulphureus*; this applies also to the fibrous tissue outside the leptome. The peduncle, as usual, is considerably stronger towards the time for the ripening of the fruit than at an ealier stage (Fig. 25, *D*), and it is somewhat stronger in *R. nivalis* than in *R. sulphureus*; in the former it is also more strongly furrowed. Consequently, judging from my material,

the difference, recorded by Simmons (l. c.), in the direction of the ripe stems in the two species in question apparently cannot be explained by the anatomical features. The pith was broken down throughout the entire stems.

The leaf is almost or quite glabrous. The radial walls

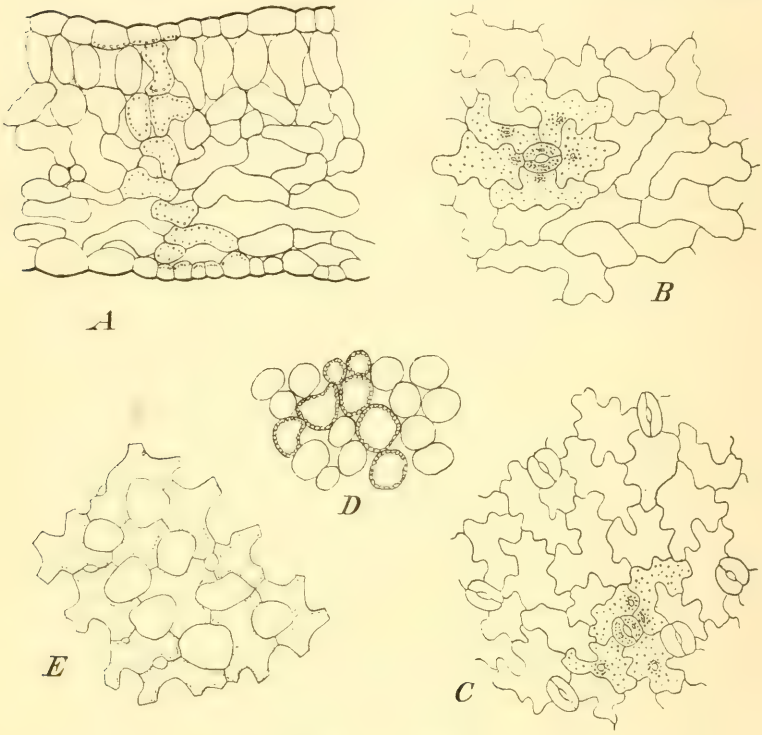

Fig 26. *R. nivalis.*

A, Transverse section of leaf. *B*, Epidermis of the upper surface. *C*, Epidermis of the lower surface. *D*, Surface section of uppermost palisade-layer. *E*, Surface section of spongy parenchyma. (*A*, *B*, *C*, *D*, *E* are from Kaafjord, Norway; $^{115}/_{1}$).

of the epidermal cells of the upper surface are somewhat undulating but less so than those of the lower surface (Fig. 26, *B*, *C*). The stomata are on a level with the surface and occur in greater numbers upon the lower surface. The relations between the numbers upon the upper and lower surface is somewhat uncertain; Börgesen (l. c. p. 229) found 4 and 11

respectively per unit of surface, Resvoll (l. c. p, 357) 25 per sq. mm. upon the upper surface as against 58 per sq. mm. upon the lower surface; according to my computation there are three times as many upon the lower, as upon the upper surface. The stomata are distributed fairly evenly over the whole surface, but they are less numerous above the veins and just at the margin of the leaf; their direction on the leaf-lobes is almost parallel with that of the main vein, but less regularly so upon the rest of the surface. The bundles are without stereom, only the larger ones upon the upper and lower surface are accompanied by a few elongated, cylindrical cells without thickened walls; each bundle is accompanied by a sheath in which the chlorophyll appears especially to lie against the outer wall.

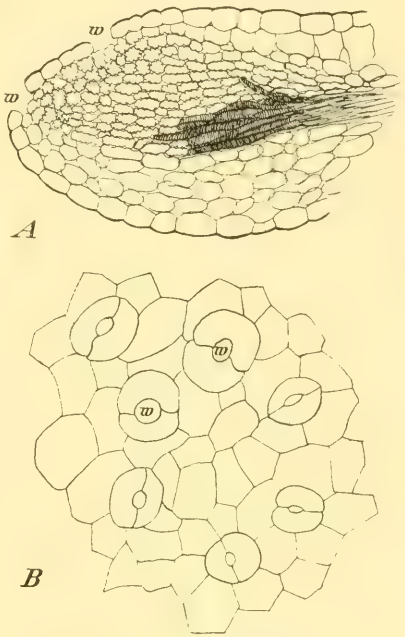

Fig. 27. *R. nivalis.*
A, Longitudinal section of leaf-apex with epithema (Spitzbergen; $^{100}/_{1}$); *w*, openings in the epidermis probably answering to the collapsed guard-cells of the water-stomata. *B*, Portion of the area with water-stomata (Disco; $^{220}/_{1}$); *w*, the apertures of the water-stomata.

From one to two palisade-layers occur which are slightly inclined towards the leaf-apex; the individual cells are about twice as long as they are thick and are often barrel-shaped and somewhat irregular; the palisade-layers constitute about one-half of the mesophyll. There is a gradual transition from the palisade-to the spongy tissue with numerous large intercellular spaces (Fig. 26, *A*); the cells are branched, which is best seen in surface section (Fig. 26 *E*). There often occurs a slit-like lacuna between the

subepidermal layer of the lower surface and the rest of the mesophyll.

In Fig. 27, *A* the epithema of the leaf-apex is shown; it is peculiar owing to the highly undulating cell-walls. The water-pores occur upon the slanting, upturned terminal surface (Fig. 27, *B*).

I found no essential differences in leaves from the different regions. It is an interesting fact which is pointed out by Börgesen, namely that the structure of the leaf becomes looser with increase of the geographical latitude (Dovre—Kaafjord (70° N. lat.) — Nova Zembla).

The leaf-stalk is reniform in transverse section. There are three vascular bundles and a large central lacuna.

R. pygmæus Wahlenb.

Lit. Buchenau & Focke, 1872, p. 28. Lange, 1880, p. 55; 1887, p. 254. Nathorst, 1884, p. 46, tab. 1. Lindman, 1887. pp. 25, 41, 100, tab. 1, fig. 7 A. B. Rosenvinge, 1892, p. 675. Wagner, 1892, pp. 8, 20. Hartz, 1894, p. 52; 1895, II, p. 288. Borgesen, 1895, pp. 255. 236. Norman, 1895, p. 11. Ekstam, 1897, p. 145. Abromeit, 1899, p. 30. Ekstam, 1899, pp. 22, 32, 37. Resvoll, 1900, figs. 11, 26. Andersson & Hesselmann, 1901, p. 48. Cleve, A., 1901, pp. 51, 78, 88, 103. Dusén, 1901, p. 30. Freidenfelt, 1904, p. 53. Sylvén, 1906, p. 272.

Alcohol material from Greenland (Danmarks Ø, Aug. 1891: Godhavn in Disco, 20. 7. 1884; Kutdlisat in Disco, 9. 8. 1890 [var. *Langeana*]; Norge (Trondfjældet Jemtland, 19. 6. 1880); Spitzbergen (Advent Bay, 3. 8. 1810; Middelhook in Belsund, 1. 7. 1882).

R. pygmæus is a perennial herb. The rhizome is vertical; roots arise from the whole of its surface and it is covered with a dense matting of the vascular strands of dead leaves. Though the rhizome does not become long yet some are commonly found measuring as much as 2 cm. in length. The plant often grows in dense tufts which are produced by the rhizomes branching freely and the individual shoots readily become de-

tached by dying away at their base. Branching takes place from the upper leaf-axils in the rosette; the principal bud occurs in the uppermost. The shoot bears first two transversely placed long-stalked foliage-leaves, then similar leaves succeed in a $\frac{2}{5}$ spiral. The principal bud frequently flowers the same year as the parent-axis, and in that case the bud which lives through the winter is seated in the uppermost leaf-axil at the base of axis II. Usually there are two stem-leaves, of which the lower is short-stalked and sometimes subtends a floral axis. Antidromy is no doubt the most common condition. (Fig. 28, *A*).

Fig. 28, *A*. *Ran. pygmæus.* (Trondfjæld in Norway; 2. 8. 1883, about nat. size). *B*. *Ran. pygmæus* var. *Langeana Nath.* (Disco: Unartok; 14. 8. 1890; about nat. size).

A, B, C, Old axes from 1882; *a, b, c,* axes that have flowered, 1883; *an, bn, cn,* their uppermost basal leaves; *α, γ,* shoots in the axils of *an* and *cn*.

I have observed only foliage-leaves on mature shoots; but a section through the principal bud from a specimen from Disco, gathered in August, showed a leaf which no doubt was a scale-leaf (Fig. 29, *A*), and Sylvén found scale-leaves upon his cultivated plants. The large leaf-sheaths of the rosette must protect the young apex of the shoot with its delicate organs during winter,

and the dense growth of the plant may also be useful in this respect.

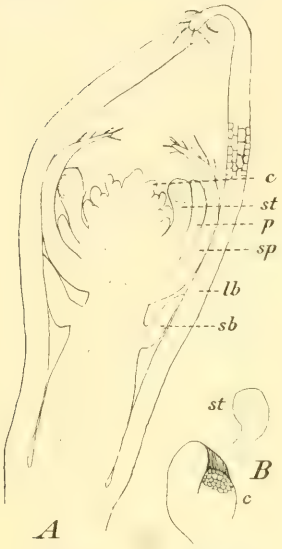

Fig. 29. *R. pygmæus.*

A, Longitudinal section through a principal bud (Danmarks Ø; Aug. 1891; $^{20}/_{1}$). *c*, Carpel; *st*, stamen; *p*, nectary-leaf; *sp*, perigone-leaf; *lb*, scale-leaf; *sb*, stem-leaf. *B*, Stamen ($^{25}/_{1}$) and carpel ($^{72}/_{1}$) from the same bud.

It is not uncommon to find plants with dead stems from the preceding year upon them (Fig. 28, *A*), which proves that at least these specimens live longer than one year (compare the statement ♃ (⊙?) in Neuman, "Sverriges flora," Lund, 1901).

The rosette-leaves, and also the lowermost stem-leaf, are stalked, somewhat reniform in shape, and deeply tripartite with either entire or shallowly 2—3 lobed elliptical segments. The 1—2 upper leaves are sessile and tripartite with oblong lobes. The leaves are glabrous or also slightly hairy at the margin.

The stem is ascending: before and just after flowering it is short, in dwarf specimens from Advent Bay in Spitzbergen about 0·5 cm.; afterwards it elongates greatly and becomes as much as 16 cm.

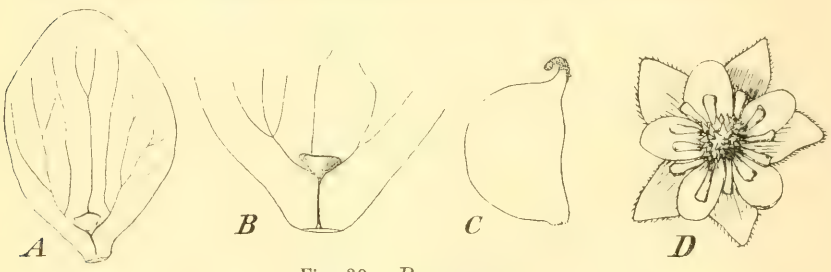

Fig. 30. *R. pygmæus.*

A, Nectary-leaf ($^{9}/_{1}$). *B*, Nectary ($^{15}/_{1}$). *C*, Fruit (Danmarks Ø; Aug. 1891; $^{15}/_{1}$). *D*, Flower of *R. pygmæus* (Holstensborg in Greenland; D, drawn by E. W.; $^{7}/_{2}$).

high. The peduncle differs from the stem in being more densely hairy and more deeply furrowed.

The flower has five slightly hairy perigone-leaves and five lustreless nectary-leaves; the anthers are extrorse or slightly turned sideways; the stamens are few in number, (Fig. 30, *D*). Ekstam found homogamy and spontaneous self-pollination to occur in Spitzbergen. Lindman also records homogamy and figures two kinds of flowers: large ones measuring about 7 mm. in diameter in which the head of carpels is so high that only the lowermost stigmas may be reached by the stamens, and small ones about 4 mm. in diameter in which the stamens stand at the same level as the head of carpels. In Spitzbergen the diameter of the flower is 5—8 mm. (Ekstam); in Nova Zembla 5—10 mm. (Ekstam). The nectaries are simple and pocket-shaped (Fig. 30, *B*). Lindman and Ekstam did not notice any perfume.

Flowering takes place in the beginning and middle of summer. In Arctic Norway the plant grows by preference at the snow-line, and the time for the coming out of the leaves may differ greatly even in the case of plants standing close to each other, according as to whether they stand nearer or further from the snow (Norman). The fruit ripens in August.

The fruit (Fig. 30, *C*) is dispersed by the agency of the wind, which may be connected with the fact of the peduncle elongating greatly during fruit-setting; but the dispersal is not very effectual and the plant is often found growing in colonies (Ekstam; 1897).

Sylvén described the germination, which takes place during spring (Cleve). Heterophylly is more decided than in *R. nivalis,* not until during the second year do the leaves attain the fully-developed form.

Nathorst has established a var. *Langeana* which is characterized by the leaf-segments of the basal leaves, and sometimes of the lower stem-leaf, being stalked. The middle lobe is 3—4 partite, and the lateral lobes are more or less symmetrically 2—4 partite (Fig. 28, *B*). The stem-leaves are almost sessile

and divided to the base into 3—5 lanceolate-oblong segments. This variety grows in mossy bogs and often together with the principal form. Hartz found numerous transitional forms between the variety and the principal form (1, p. 52). Nathorst found this variety on Disco, where Hartz also found it as he also did on Arveprinsens Island.

In var. *Langeana* it often happens that the internodes of the rosettes are elongated, in correspondence to its life in quickly-growing moss.

Geographical Distribution. West and East Greenland, Iceland, Scandinavia, Beeren Eiland, Spitzbergen, Nova Zembla, Arctic Russia, North Siberia, Arctic North America, the Rocky Mountains (Lange, Th. Holm).

Anatomy. The root of the first order was diarch or triarch. The epidermis was more or less collapsed especially in roots of the second order. The exodermis was distinct, the latter and the epidermis were suberized. The outermost layers of the cortex were either not at all collenchymatously thickened or but very slightly; its intercellular spaces were fairly large; lysigenous lacunæ often occur, especially in roots of the second order. The endodermis was suberized but not thickened.

Mycorrhizas have been found in specimens from Advent Bay, Trondfjældet and Disco. The hyphæ often form balls in the inner cortical layers, especially in roots of the second order.

The greater part of the epidermis of the rhizome had fallen off in the specimens investigated; the outer cortical layers were suberized and slightly thickened. Lacunæ were absent from the cortex. 5—8 vascular bundles which anastomosed freely were present; and also, in different sections of the same root, isolated bundles were seen with a special endodermis; also groups of bundles, each group with its own endodermis; or else all the bundles were fused together so that there was an outer and an inner endodermis, between which the bundles occurred (Fig. 31, *A*). The cambium was rudimentary. The vessels were scattered among non-lignified paren-

chyma. The pith was not broken down. The starch-grains were highly compound.

The stereom in the stem is weak during flowering but afterwards — when the peduncle elongates greatly — it becomes much stronger: it is about four layers thick between the bundles which, upon their inner sides, are often surrounded by lignified parenchyma and upon their outer sides by strong fibrous tissue. Between the woody part and the inner arch there occurs in the larger bundles a quantity of small-celled, non-lignified parenchyma (p) as in the majority of the other species; and between the vessels and the cambium occurs some wood-paren-

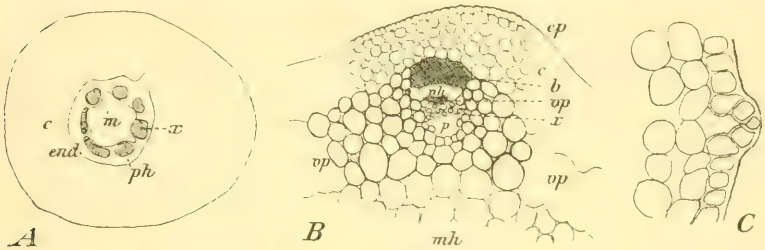

Fig. 31. *R. pygmæus.*

A, Transverse section of rhizome (Spitzbergen; $^{23}/_{1}$). *B*, Portion of transverse section of stem (Spitzbergen; $^{72}/_{1}$). *C*, Stoma from the stem (Danmarks Ø; $^{220}/_{1}$). *ep*, Epidermis; *c*, cortex; *end*, endodermis; *b*, bast; *ph*, leptome: *vd*, lignified parenchyma; *x*, xylem; *p*, parenchyma; *m*, pith.

chyma. The vessels were but slightly developed in the specimens investigated, their diameter is small, and they are few in number. The cambium is rudimentary. The bundles number 5—8. The pith breaks down gradually but entirely (Fig. 31, *B*).

The cortex consists of cylindrical cells and has large intercellular spaces. The stomata are on a level with the surface or project slightly (Fig. 31, *C*); the cuticle is slightly striped; chlorophyll is present in the epidermis.

The leaf nearly resembles in structure that of *R. nivalis;* the thickness varies from 270 to 300 μ. The radial walls of the cells of the upper and lower epidermis are somewhat undulating, those of the lower somewhat more so than those of the upper

(Fig. 32, *B*, *C*). The stomata are either on a level with the surface or project slightly. Borgesen and Wagner record the number to be equal upon both surfaces, Resvoll records 44 per sq. mm. upon the upper as against 62 per sq. mm. upon the lower surface. Chlorophyll is present in the epidermis. From one to two layers of palisade-cells occur which are scarcely twice as high as they are broad and are somewhat barrel-shaped;

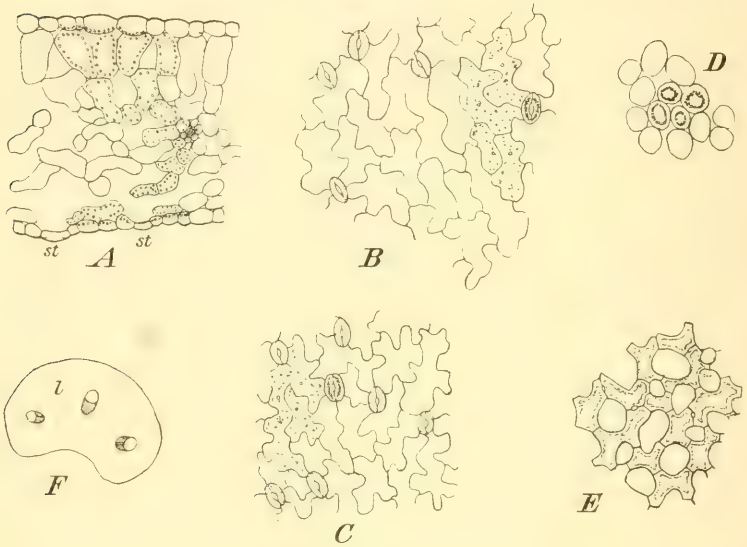

Fig. 32. *R. pygmæus.*

A, Transverse section of leaf (Danmarks Ö; $^{100}/_{1}$). *B*, Epidermis of the upper surface of the leaf (ibid; $^{110}/_{1}$). *C*, Epidermis of the lower surface of the leaf (ibid; $^{110}/_{1}$). *D*, Surface section of palisade-layers (ibid.; $^{110}/_{1}$). *E*, Surface section of spongy parenchyma (ibid.; $^{110}/_{1}$). *F*, Transverse section of leaf-stalk ($^{22}/_{1}$).

they constitute from $^{1}/_{3}$ to $^{1}/_{4}$ of the thickness of the mesophyll. The spongy parenchyma consists of branched cells and is very loose in structure especially in its lower part where large slit-like lacunæ are often seen between the subepidermal layer and the rest of the mesophyll; (Fig. 32, *A*, *D*, *E*). The bundles are not accompanied by stereom and are surrounded by a sheath containing chlorophyll.

Each leaf-apex terminates in an epithema the structure

of which is similar to that of *R. nivalis* and, as in the latter, the area with the water-pores occurs almost at the margin; stomata are absent from the under side of the leaf-apex.

The leaf-stalk is reniform in transverse section. There are three vascular bundles; they are without stereom. The cortex often has lacunæ, but otherwise resembles that of the stem (Fig. 32, *F.*).

R. reptans L.

Lit. Lange, 1887. Hartz, 1894, p. 34. Norman, 1895, p. 6. Rosenvinge, III, 1896, p. 240.

Alcohol material from Greenland (Sophiehamn, 6. 8. 1883; Monekordhiak, 19. 7. 1883); Denmark (Fure Sø, 2. 9. 1910).

R. reptans from a morphological point of view, is a transitional form between the preceding species and the *R. lapponicus*-type. In the flowering plant there is a short, erect rhizome which bears a rosette consisting of a few, stalked, linear to linear-lanceolate foliage-leaves, the uppermost of which subtends a principal bud which may develop a floral-stem with elongated internodes the same year as the parent-axis flowers, but which no doubt usually develops only a rosette. I am not prepared to say whether the latter may remain green during winter in Arctic countries; in Denmark it passes the winter in a green condition.

The more or less filiform ærial stem becomes horizontal with the formation of the first elongated internode. The internodes are highly curved as in *R. hyperboreus*. The two-rowed leaves are very similar in form to the rosette-leaves and, like the latter, they have a large sheath; the uppermost ones are very small, the number of leaves on the straight stem differs much, I have in arctic specimens often found 3—5 but 14 also occurs; the creeping stem may reach the length of about 50 cm. When the axis flowers it becomes ascending, usually just above the uppermost leaf; the peduncle however often bears a bract. The uppermost leaf upon the horizontal

stem may subtend a shoot with elongated internodes, which continues the main axis sympodially until that also produces a flower, and so on. But in Greenland and Iceland, judging from herbarium-material, it seems probable that rarely more than two generations of axes attain the flowering stage. In the other axillary-shoots of the stem the internodes either remain short or the axillary shoots develop like the parent-axis and flower; their axillary shoots are rosettes; this is also frequently the case with the main shoot.

The more vigorous shoots occur in the lower axils of the straight stem, and from their bases and from the nodes of the parent-axis vigorous adventitious roots arise late in summer. They are of two kinds: some slender, hyaline and abundantly branching, and others which are white and almost unbranched and begin with a somewhat thickened base, becoming thinner downwards; these roots may be regarded as storehouses of food-material for the axillary-shoots which become independent during autumn by the death of the parent-axis.

The flower has five somewhat prominent perigone-leaves and five yellow nectary-leaves which do not overlap and are somewhat longer than the perigone-leaves (from 2·5 to 6 mm.). The nectaries are simple and pocket-shaped (Fig. 33). The anthers are turned sideways. The cluster of ovaries is almost globular and does not overtop the stamens. In the material, both from Greenland and Denmark, the flowers were somewhat protandrous-homogamous. The diameter of the flower in Arctic Norway is about 9 mm. (Norman), in Greenland and in Denmark about 5 mm. The time of flowering in Arctic Norway is from the middle of July to September, and in Denmark from the middle of June to the middle of September.

Fig. 33. *R. reptans.* Nectary-leaf (Greenland; $^{6}/_{1}$).

The ripe fruits have a more or less curved beak, and if they are not wetted, can float for a long time (from one to

two weeks), but the majority of them sink within 48 hours if the surface gets wet (according to my experiments, made with Danish fruits[1]). I can make no statement about the germination, but the fruits of the nearly allied *R. Flammula* are capable of germinating immediately after maturation.

R. reptans grows on the pebbly shores of lakes, where it often forms a dense mat; it may also occur among moss (Hartz); it is often submerged and the leaves are then linear and it is sterile; Norman records that in Arctic Norway it may be found in large expanses of water at a depth of as much as one metre. According to Norman it is a decidedly continental plant in Arctic Norway in the greatest contrast to *R. Flammula*.

Geographical Distribution. North America, from Canada and Newfoundland to 69° N. lat.; West Greenland; Iceland; the Færoes; Central Europe; Scandinavia, as far as Finmark; Finland and Arctic Russia. (Lange).

Anatomy. The root resembles in structure that of other species of *Ranunculus*. Roots containing reserve food-material (of which only Danish specimens have been investigated) have a still entire epidermis; the exodermis is of somewhat radially elongated cells with undulating walls; both the layers are suberized. The cortex has no thickened outer layers; its cells are full of starch (the grains are compound). The endodermis is suberized but the walls are not thickened. The central cylinder is diarch, the vessels are slightly developed. The slender roots have a more or less collapsed epidermis and the cortex is for the greater part broken down. The central cylinder is also diarch in these roots. The diameter of the central cylinder relative to that of the root is only slightly smaller in the roots containing reserve food-material than it is in the slender ones.

Mycorrhizas have not been found.

The nodes and the internodes of the stem differ some-

[1] See also Kolpin Ravn: Om Flydeevnen hos Frøene af vore Vand- og Sumpplanter. Bot. Tidsskrift, Bd. 19, København, p. 146.

what in structure, the former having become rhizome-like by the anastomosing bundles coming closer to each other, so that the cortex is thicker than in the internodes. The cortex and the pith are not broken down and lignification often occurs in the latter in the Danish specimens. The bundles are without stereom. The internodes are somewhat different in structure in the Danish specimens, according as to whether the land-or the submerged form is in question. The bundles in the latter are not accompanied by stereom, while the former has an external weak, and an internal stronger arch of bast and of lignified parenchyma respectively (Fig. 34, *b* and *vp*). The specimens from Greenland were similar in structure to the Danish land-form. The bundles number from three to seven. The vessels are few in number, but large. Some small-celled parenchyma occurs between the vessels and the inner arch, and some wood-parenchyma between the vessels and the sieve-tissue. No interfascicular lignified parenchyma occurs. The endodermis is indistinct. The pith is broken down in all the specimens which have been investigated from all localities. The epidermal cells have only slightly thickened walls, but they are thicker in the land-form than in the submerged form, and the former has also a more distinctly striped cuticle than has the latter. The living cortex consists everywhere of but 2—4 layers.

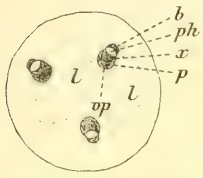

Fig. 34. *R. reptans.* Transverse section of an internode of the stem of the land-form (Denmark $^{20}/_{1}$); *b*, bast; *ph*, leptome; *x*, xylem.; *p*, parenchyma, *vp*, wood-parenchyma; *l*, lacuna.

The structure of the leaf varies greatly according to external conditions. As there is a gradual transition from the submerged, linear leaf to the linear-lanceolate leaf of the land-form, so there is also from the nearly radial to the dorsiventral. The dorsiventral leaf (Fig. 35, *A*) has one palisade-layer the cells of which are barrel-shaped and somewhat irregular; they form about one-half of the thickness of the leaf. There is a gradual transition to the spongy cells, which are slightly bran-

ched. The epidermal cells have undulating radial walls. The stomata are more numerous upon the upper surface, but the number varies somewhat in the different leaves. In the specimens from Denmark I found from 57 to 83 per sq. mm. upon the upper surface, and about 50 per sq. mm. upon the lower, and the specimens from Greenland have about the same number.

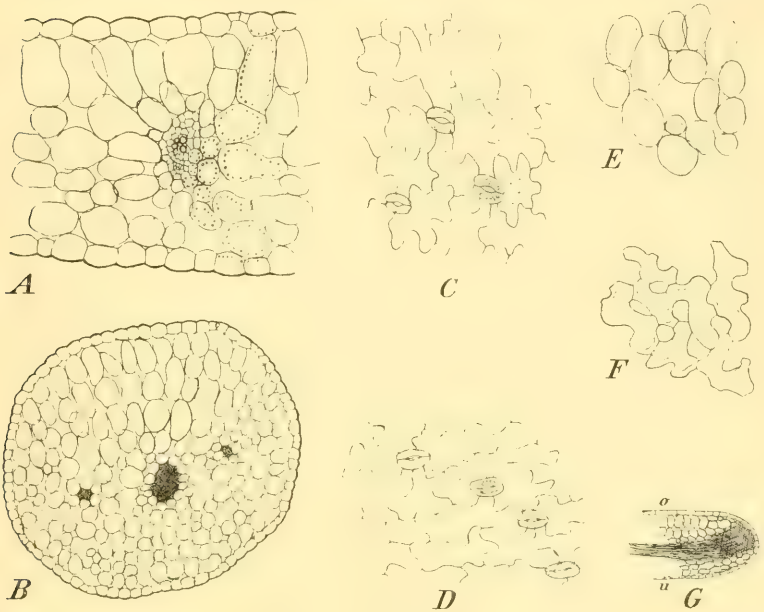

Fig. 35. *R. reptans.*

A, Fragment of transverse section of leaf of land-form (Denmark; $^{110}/_{1}$). *B*, Transverse section of leaf of submerged form (Denmark; $^{110}/_{1}$). *C*, Epidermis of the upper surface of leaf of land-form (Denmark; $^{24}/_{1}$). *D*, Epidermis of the lower surface of leaf of land-form (Denmark; $^{24}/_{1}$). *E*, Surface section of palisade-cells of land-form (Denmark; $^{94}/_{1}$), *F*, Surface section of spongy parenchyma of land-form (Denmark; $^{94}/_{1}$). *G*, Longitudinal section through the leaf-apex of land-form (Denmark; $^{26}/_{1}$).

In the Danish specimens there is also some chlorophyll in the epidermis; (Fig. 35, *C*, *D*). A few thick-walled hairs of the usual type occur. The bundles are without stereom. The radial leaf is rounded and has an axile bundle. The mesophyll and the epidermis consist of elongated cylindrical cells; stomata are present, but in no great number. This leaf resembles that of *Batrachium*, but has larger intercellular spaces. Fig. 35, *B*

shows a leaf transitional between the two types; the mesophyll of the upper surface is palisade-like, and there are three bundles. The bundles are without stereom, but have a more or less distinct sheath containing chlorophyll.

Each leaf-apex has an epithema which opens at the margin (Fig. 35, *G*). The cells have highly undulating walls, similar on the whole to those in *R. nivalis*.

R. hyperboreus Rottb.

Lit. Hooker, 1833. Lindman, 1887, p. 41, fig. 8 a, b, tab. I. Hartz, 1894, pp. 6, 34; 1895, (II), p. 289. Norman, 1895, p. 8. Rosenvinge, I, 1892, p. 675; III, 1896, p. 108. Kruuse, 1897, p. 385. Abromeit, 1899, p. 30. Andersson & Hesselman, 1900, p. 47. Resvoll, 1900, figs., 4, 5, 13, 20, 22, 23, 25, 27, 28, 30, 33. Dusén, 1901, p. 30. Porsild, 1902, pp. 170, 196, 205. Simmons, 1906, p. 115.

Alcohol material from Greenland (Friedrichsthal, 29. 8. 1883, Jacobshavn, 25. 7. 1884, Sermilik, 3. 7. 1885, Kingigtortadlit, 1. 7. 1887, Uperniviarsuk, 9. 7. 1887, Niodluisuk-Øen, 21. 8. 1888). Iceland (Thingvellir, 13. 6. 1895). Lapmark (Bosekob, 3. 7. 1884). Spitzbergen (Gåseöen 28. 7. 1882).

R. hyperboreus bears a great resemblance to *R. lapponicus* but is distinguished from the latter *inter alia* by the form of its leaf, by its more abundant branching, and by its much shorter flower-stalks. The leaf is deeply tripartite, the lobes are narrower than in *R. lapponicus,* the middle one is entire and the lateral lobes are often shallowly 2-lobed (Fig. 36). The leaves are placed in two rows upon the slender stem the internodes of which are curved. The internodes may reach a length of 10 cm. Usually every leaf subtends a lateral shoot which is antidromous to the main axis. The first leaf of the shoot is situated dorsally and somewhat sideways, and its internode is elongated. It is no doubt usual for 3—4 generations of axes to attain the flowering-stage during the same year; the first

ones produce both leaves and flowers, the higher ones are often purely floral, with sessile bracts and short internodes.

Roots arise from the nodes of the stem; they may attain a great length (20 cm.) and are usually unbranched.

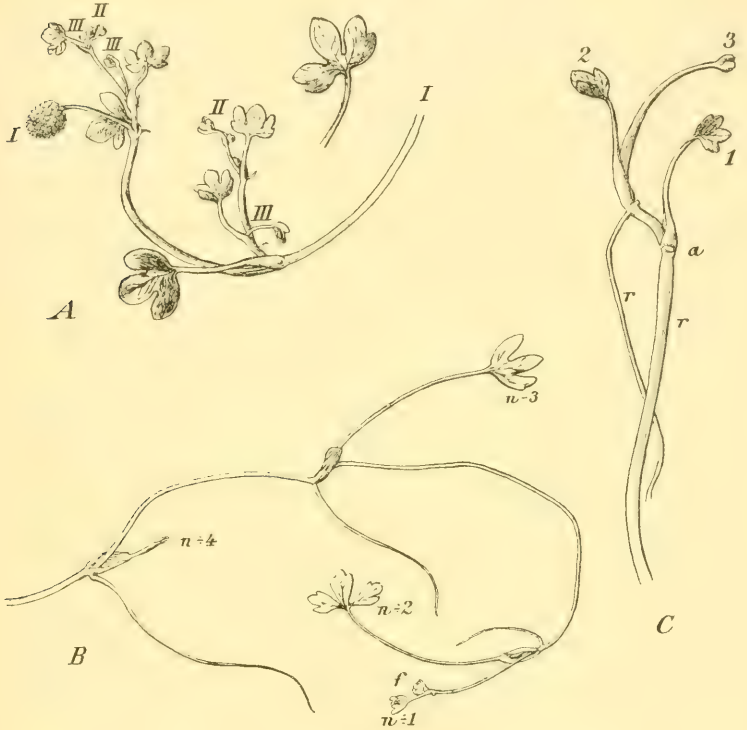

Fig. 36. *Ran. hyperboreus.*

A, A specimen from Friedrichsthal; about nat. size. *I* is the main axis which has flowered, the two last leaves subtend lateral axes (*II*) which bear flower-buds. Axes of the third order have begun to develop. A leaf is seen above. *B*, A somewhat etiolated plant which has probably just quitted the winter condition; leaf $n \div 4$ is dead, as also the leafy axis which occurs behind it; the leaves $n \div 5$ and $n \div 6$ (omitted from the figure) subtended lateral axes which now are independent. (Kingigtortadlit 1. 7. 1887; about nat. size). *C*, Gemmule (Spitzbergen: Gåseö; 1/1); *r*, root; *a*, scar, answering to the point of attachment to the parent-axis.

R. hyperboreus passes the winter without visible means of protection. Plants which have just begun to grow in spring, have long, slender, and apparently etiolated shoots from the dead stem of the preceding year (Fig. 36, *B*).

The flowers are small and short-stalked and the leaves

project above them (Abromeit). The perigone-and the nectary-leaves are usually trimerous (Fig. 37); but the pentamerous condition may also occur; the perigone-leaves are yellowish and highly arched, the nectary-leaves are yellow; the nectar-pocket is simple (Fig. 38, *A*). The stamens number from a few to about 20; they are short and can reach only the lowest carpels (Lindman). In Norway the homogamy of the flower is preceded by a short staminate stage (Lindman); Warming (note-book) found it to be homogamous in Greenland. In Ellesmeresland Simmons searched in vain for expanded flowers; the flower-buds, as also the fruit-clusters, were always submerged,

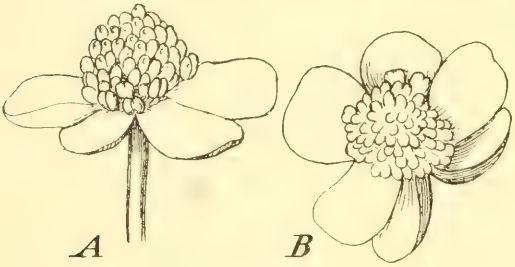

Fig. 37. *Ran. hyperboreus.*
A, B, Flowers from Greenland; (drawn by E. W.; 1/1).

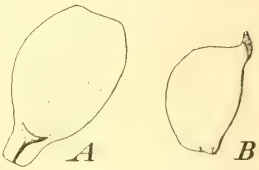

Fig. 38. *Ran. hyperboreus.*
A, Nectary-leaf (8/1). *B,* Fruit (8/1).

therefore he thinks that the flowers are cleistogamous and that self-pollination takes place below the surface of the water. The flower is often sterile (Kruuse, Anders. & Hesselm.); the time of flowering is July and August.

Vegetative propagation is the more usual method: new individuals are formed by the lateral shoots becoming independent upon the decay of the parent-axis. Perhaps gemmules also are important to the process. Fig. 36, *C* shows a gemmule from Gåseøen (Spitzbergen). At the point of transition between the stem and the large root an oval scar is seen, the place of connection with the parent-axis. I saw only this one, but it is possible that axillary shoots are normally set free from the parent-axis before they develop further.

Geographical Distribution. East and West Greenland,

Arctic North America with the Archipelago, Labrador, the Rocky Mountains, Arctic Siberia, the Himalayas, Arctic Russia, Nova Zembla, Spitzbergen, Northern Scandinavia, Iceland (Simmons).

Anatomy. The epidermis of the roots is thin-walled and the walls are collapsed; the exodermis has undulating radial walls; both layers are suberized. The cortex is almost entirely broken down even in roots picked during the early part of summer, only a few layers remaining within the exodermis and around the suberized, thin-walled endodermis. The central cylinder is diarch. Root-hairs are present but few in number; I have not found mycorrhiza.

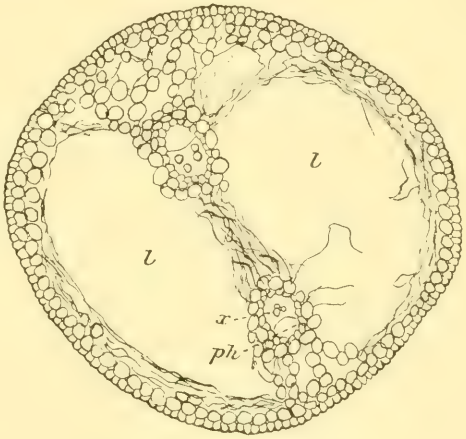

Fig. 39. *Ran. hyperboreus.*
Transverse section of the prostrate stem (Uperniviarsuk. *ph*, Leptome; *x*, xylem; *l*, lacuna.

The stem is rounded and smooth, the cuticle is slightly striped, and the outer walls of the epidermal cells are thin; the stomata are on a level with the surface or project slightly; the epidermis contains chlorophyll. Anatomically the stem may be divided into two parts, viz. the nodes which have the usual structure of the rhizome (see *R. lapponicus* p. 401) and the internodes. The latter are exceedingly loose in structure with large intercellular spaces; the greater part of the cortex and the pith is broken down at an early stage (Fig. 39), but the extent of disorganisation is no doubt somewhat dependent upon the locality. The 2—4 bundles are either quite devoid of stereom or else they have fibrous tissue outside the leptome consisting of some weak strands of bast. The structure of the peduncle

is not, in any essential degree, stronger than that of the prostrate stem, only there is a larger amount of close-set parenchyma, which becomes lignified around the bundles during fruit-setting; also in the peduncle the pith and the cortex are usually broken down; the subepidermal layer is placed close to the epidermis.

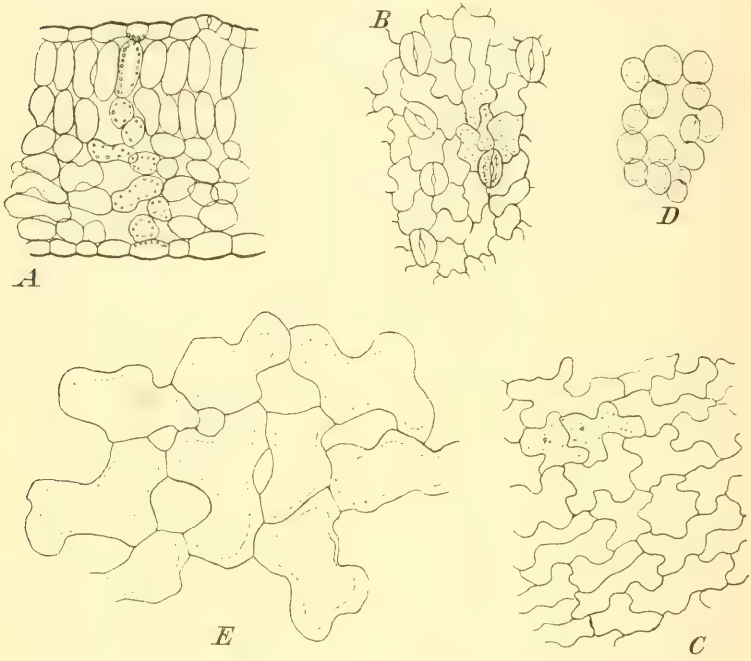

Fig. 40. *Ran. hyperboreus.*

A, Transverse section of leaf (Thingvellir; $^{146}/_{1}$). *B*, The epidermis of the upper surface (Greenland; $^{130}/_{1}$). *C*, The epidermis of the lower surface (Spitzbergen; $^{154}/_{1}$). *D*, Surface section of palisade-cells (Greenland; $^{130}/_{1}$). *E*, Surface section of spongy parenchyma (Greenland; $^{339}/_{1}$).

The leaf is glabrous; the thickness varies from 180 to 270 μ. The cells of the epidermis have undulating anticlinal walls, those of the upper surface often somewhat more so than those of the lower; chlorophyll is present. The stomata are on a level with the surface; they vary greatly in number, but are always most numerous upon the upper side. In specimens from Nidluitsukøen and Gåseøen (Spitzbergen) they were almost

entirely absent from the lower surface, but occurred to the number of about 100 per sq. mm. upon the upper surface. Resvoll records concerning specimens from Jacobshavn in Greenland that they have none upon the lower and 126 per sq. mm. upon the upper surface; and in those from an unnamed locality in East Greenland, 27 upon the lower as against 235 upon each sq. mm. of the upper surface; and in specimens from Bosekob, 34 on the lower surface as against 63 per sq. mm. of the upper surface. Two palisade-layers usually occur, constituting about one-half of the mesophyll; the individual cells are about twice as long as they are thick, are barrel-shaped and somewhat irregular. There is a gradual transition from the palisade-layers to the spongy parenchyma which consists of slightly branching cells and has numerous intercellular spaces (Fig. 40, *A*). The sub-epidermal layer which is placed close to the epidermis has cells which often branch more abundantly than those of the rest of the spongy parenchyma. The bundles are not accompanied by stereom.

The area with the water-pores is situated almost at the margin. The structure of the epithema is as in *R. lapponicus*.

The specimen from Thingvellier was somewhat more compact in structure and had slightly longer palisade-cells than the rest of the specimens investigated.

The leaf-stalk was like that of *R. lapponicus*.

Ranunculus lapponicus L.

Lit. Hooker, 1833, I, p. 16. Hartz, 1894, p. 36. Norman, 1895, p. 10. Borgesen, 1895, pp. 236, 37. Ekstam, 1897, p. 145. Abromeit, 1899, p. 31. Ekstam, 1899, p. 22. Resvoll, 1900, figs. 7, 15, 19, 21, 24, 29, 34. Andersson & Hesselman, 1901, p. 47.

Alcohol material from Spitzbergen (Rendalen in Sassenbay, 15. 7. 1882); Greenland (Kororsuak, 19. 6. 1879; Sarfanguak (Holstenborg), 21. 7. 1884; Kappinilik, 5. 9. 1885; Christianshaab, 2. 7. 1888).

Ranunculus lapponicus is a perennial, creeping herb. The pale, horizontal stem which creeps in the moss dies away at the hinder end but keeps on growing sympodially by means of the principal bud situated in either the uppermost leaf-axil or the one below it. Above the principal bud the main axis becomes negatively geotropic, bends upwards, and produces a flower.

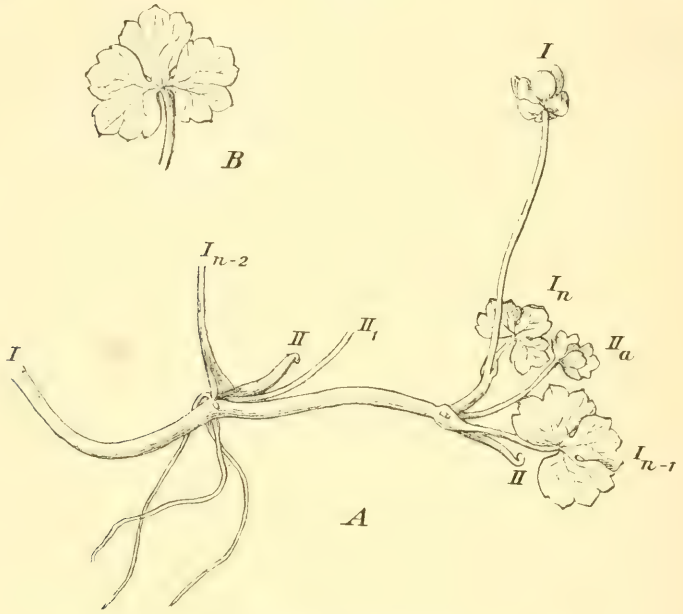

Fig. 41. *R. lapponicus.* (Spitzbergen; 15.7.1882).

A, (1/1), The flowering axis bears the leaves *In*, *In*-1, *In*-2; the last two subtend vegetative buds which bear the leaves II_1 and IIa; the uppermost lateral axis may be regarded as a principal bud. *B*, A foliage-leaf (1/1).

The first stage of the plant is probably similar to that of *R. reptans*: a rosette of leaves upon a short vertical rhizome and a prostrate main axis which gives off roots from the nodes. This main axis no doubt soon becomes independent as the rosette dies, and then it continues its growth as described above. The filiform roots which arise from the nodes are usually unbranched and may be very long, as much as about

20 cm.; they are developed during the same year as the rhizome upon which they occur. The arrangement of the leaves is two-rowed; they are long-stalked, reniform and tripartite with 3—5 broad shallowly-lobed segments.

Usually only the principal bud develops. The first internode of the shoot is quite short, and the first leaf is dorsolateral; the following internodes are elongated. The end of the shoot terminates in a hook formed by an unexpanded revolute leaf, the sheath of which surrounds the apex of the stem. This apex, in herbarium-specimens, is often seen directed obliquely downward. The horizontal rhizome may attain a length of as much as about 22 cm. In many of the individuals which I have had for examination the erect or ascending main and flowering axis bore a barren leaf (Fig. 41); Hooker (l. c.), records that in America this is the case only in specimens from the coast: this leaf is placed either high up upon the axis and is then bract-like, or else lower down and has then the form of the leaves upon the rhizome. The internode of this leaf is usually ascending and its anatomical structure is then similar to that of the flower-stalk; more rarely it is prostrate and similar in structure to the rhizome, roots being produced at the node. During fruit-setting the vertical axis elongates greatly (and reaches as much as about 16 cm.).

The flower has three green perigone-leaves which are somewhat downwardly bent in older flowers, and about seven nectary-leaves which are *Ficaria*-yellow in colour and glisten as with varnish and are only slightly longer than the perigone-leaves. The stamens are turned partly laterally and partly outwards. The ovaries are oval and somewhat flattened with a long hooked beak. The nectaries are simple and pocket-shaped (Fig. 42).

According to Warming's notes (Sarfanguak, 14. 7. 84) the carpels and the stamens ripen simultaneously, and as the latter stand closely against the former, self-pollination must easily

take place. By bending inwards the anthers touch the stigmas and are often thrust entirely in between them, and the apices of the stigmas are often bent down outside the anthers. Ekstam found proterogyny-homogamy both in Nova Zembla and in Spitzbergen; he writes in 1897 that self-pollination is apparently impossible as the carpels are always higher than the stamens; but he finds (1899) that in Spitzbergen self-pollination easily takes place by the stigmas becoming bent spirally backwards at the time that the stamens open and bend inwards. In Greenland

Fig. 42. *R. lapponicus.*

A, Base of nectary-leaf with nectary (Greenland; $^{6}/_{1}$). *B*, Almost ripe carpel (Sarfanguak; $^{6}/_{1}$). *C*, Flower seen from above (Sarfanguak; 12. 7. 1884; $^{5}/_{2}$). *D*, Longitudinal section through flower (ibid.; $^{5}/_{2}$); the anthers stand close to the stigmas. *E*, *F*, Stamens ($^{10}/_{1}$) seen from the outer side. (*C*, *D*, *E* and *F* were drawn by E. W.).

the diameter of the flower is 10—12 mm. (Warming); in Spitzbergen 8—10, sometimes 13 mm.; in Nova Zembla 5—8 mm., and in Arctic Siberia usually 12 mm. (Ekstam, 1897 and 1899). Ekstam found that the flowers had a strong perfume in Spitzbergen, but were scentless in Nova Zembla. Hartz (l. c.) records fragrant flowers from Egedesminde. No insect-visitors have been noticed. The plant flowers July-August; ripe fruit has not been found in Spitzbergen, but it is probably formed (Ekstam, 1899; Andersson & Hesselman l. c.). Ekstam did not find ripe fruit in Nova Zembla (1897).

The fruit may be dispersed perhaps partly by the agency of animals (epizoically) and partly by the agency of the wind.

I am not prepared to state anything regarding the germination. Hooker (l. c.) records that the species reproduces itself by gemmules; my material gave no information regarding this point. Vegetative propagation takes place by the separation of lateral axes.

R. lapponicus grows in marshy localities among moss (*Sphagnum*); it appears to be rather rare wherever it occurs.

Geographical Distribution: Arctic America and Labrador, West Greenland, Spitzbergen, northern Scandinavia, Arctic Russia, Nova Zembla and northern Siberia (Nathorst l. c.).

Anatomy. The roots are usually unbranched, long and filiform. Their internal structure is exceedingly loose. There are no differences in the roots of plants from the different localities. Both the epidermis and the exodermis are suberized; towards the apex of the roots the former has thin outer walls which have a tendency to collapse, but towards the base the outer wall is of the same thickness as the rest of the walls; the latter has slightly folded radial walls. No thickened outer portion of the cortex occurs; it is often entirely broken down with the exception of a few layers of the inner and the outer cortex and the trabeculæ which connect the two last and stand opposite to the woody parts of the central cylinder. The endodermis is suberized, at any rate in the upper part of the root. There are three wood masses which, in the older root, meet in the middle. No mycorrhiza has been found. The starch-grains are compound.

The stem consists anatomically of three parts: the internodes, the nodes and the flower-stalk. The first-mentioned are characterized by the vascular bundles (3—6) not anastomosing and being almost without stereom, and by the pith and cortical tissue being very much broken down by age, as in *R. hyperboreus*. The nodes are similar in structure to those of

the rhizomes of the species with erect stems; the bundles anastomose and form a more or less complete ring around the pith; the latter and the cortex are less lacunose; the cells of the latter are somewhat tangentially elongated and there are more cortical layers than in the internodes. Roots arise from the nodes.

The flower-stalk, especially towards the time for the ripening of the fruit, is rather rich in stereom (Fig. 43). It is somewhat polygonal in transverse section. The cuticle is decidedly striped, and the stomata project above the surface. The cortex has large intercellular spaces. Each bundle (3—6) is surrounded by a sheath of stereom; there is strong fibrous tissue outside the leptome. Between the wood and the cambium there is a several-layered mass of wood-parenchyma with highly thickened walls, and between the vessels and the endodermis there is some non-lignified parenchyma. The interfascicular, lignified parenchyma is 5—6 layers thick and its walls are rather highly thickened. The pith in the peduncle is found partly broken down; its cells were slightly lignified. — The epidermal cells contain chlorophyll.

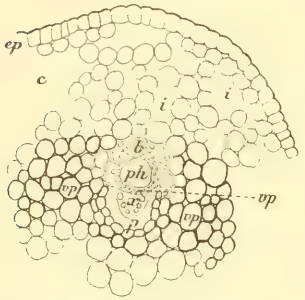

Fig. 43. *R. lapponicus.* Portion of transverse section of peduncle (Spitzbergen; $^{35}/_{1}$). *ep*. Epidermis; *c*, cortex; *i*, intercellular space; *b*, bast; *ph*, leptome; *x*, xylem; *p*, non-lignified parenchyma; *vp*, lignified parenchyma.

The leaf. The epidermal cells as usual, have only slightly thickened outer walls. The cells contain chlorophyll. Seen with the naked eye the leaf shows brown spots upon both surfaces: many of the cells of the epidermis being filled with brown juice, probably tannin (it did not, however, give the reaction with the iron-salts). The walls of the upper epidermis are slightly undulating and stomata are almost entirely absent; the walls of the lower epidermal cells are highly undulating (Fig.

44, *B*, *C*) and stomata occur in great numbers; Resvoll found 136 per sq. mm. The stomata are on a level with the surface. The epidermal cells above the larger nerves are elongated and have less undulating walls. The palisade-cells usually occur in two layers or else in only one, and are at most twice as long as they are thick; the layers, taken as a whole, constitute scarcely one-half of the thickness of the mesophyll. The individual cells are often irregular. The spongy parenchyma is loose in structure,

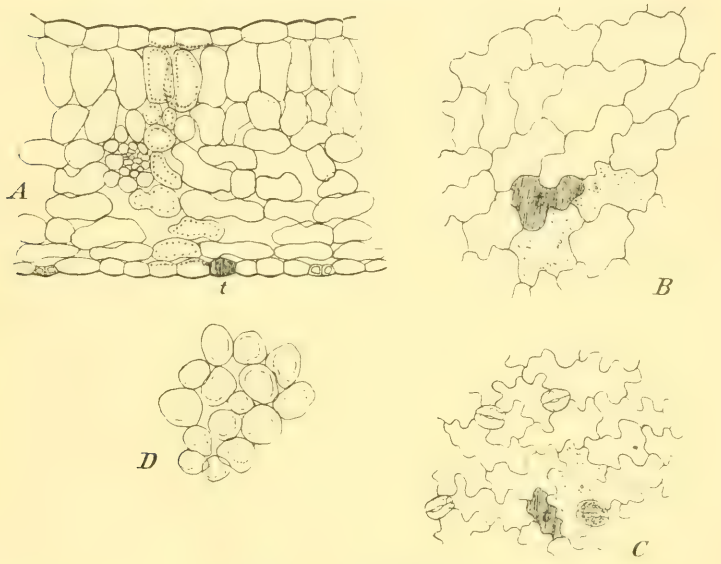

Fig. 44. *R. lapponicus.*

A, Transverse section of leaf (Sassenbay in Spitzbergen; $^{130}/_{1}$); *t*, brown-coloured cells probably containing tannin. *B*, The epidermis of the upper surface (Greenland; $^{96}/_{1}$); *t*, as in *A*. *C*, The epidermis of the lower surface (Greenland; $^{96}/_{1}$); *t*, as in *A*. *D*, Surface section of palisade-cells (Greenland; $^{130}/_{1}$).

its cells are slightly branched or polygonal (Fig 45, *A*), but the subepidermal layer consists of abundantly branching cells. There is a gradual transition from the form of the tissue of the upper to that of the tissue of the lower surface. The bundles are without stereom, but the larger ones among them upon the upper and lower surface are accompanied by elongated cells. Around each bundle there is a sheath containing chlorophyll.

In each leaf-apex there is an epithema which opens out almost at the margin, upon a slanting, upwardly-directed surface. The tracheids terminate in intercellular spaces and the cells of the epithema have short branches and undulating walls as in the other species (Fig. 45, *B*).

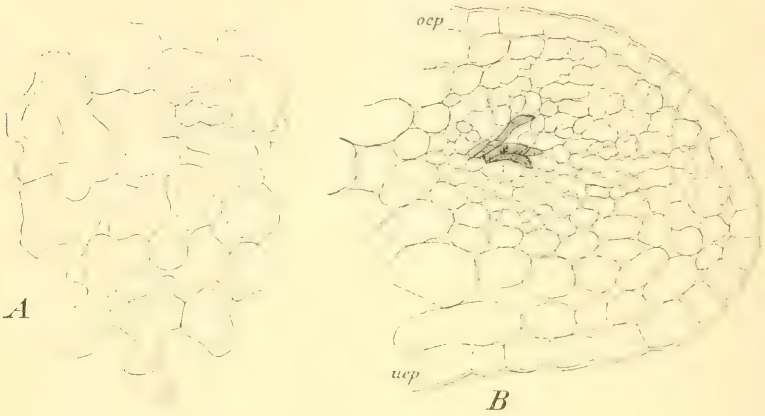

Fig. 45. *Ran. lapponicus.*

A, Surface section of spongy parenchyma (Spitzbergen; $^{153}/_{1}$). *B*, Longitudinal section of a leaf-apex (Greenland; $^{180}/_{1}$) showing the epithema and some tracheids.

The leaf-stalk has three vascular bundles, which are almost like those of the fruit-stalk in structure, but are somewhat weaker; the pith and the cortex are lacunose. The epidermis contains chlorophyll; the cuticle is furrowed.

R. Pallasii Schlecht.

and

R. lapponicus L. × *R. Pallasii* Schlecht.

Lit. Hooker, 1833. Nathorst, 1883, p. 21. Ekstam, 1899, p. 21. Andersson & Hesselman, 1901, pp. 42—47 (Figs. of leaf, leaf-anatomy, etc.).

Alcohol material from Spitzbergen. *R. Pallasii:* Advent Bay, 11. 8. 1882; the hybrid: Rendalen in Sassenbay, 15. 7. 1882.

The stem of *R. Pallasii* essentially agrees in structure with that described for *R. lapponicus*. The stem is rounded and somewhat inflated; in the horizontal portion stolons arise from the axils of the two-rowed, distant leaves; the first leaf of the shoot has often only a short internode. I do not think there is any true principal shoot. The uppermost leaf, which is smaller than the others upon the main axis, often subtends a horizontal stolon or, as in the herbarium-specimen, one with

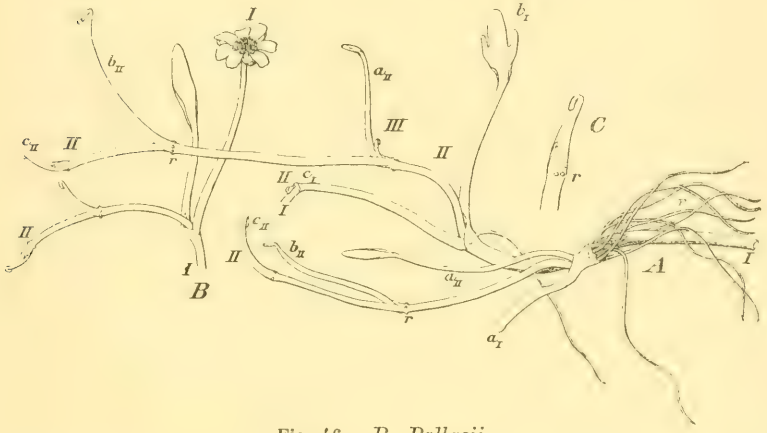

Fig. 46. *R. Pallasii.*

A. A specimen about $^2/_1$. The axes are indicated by Roman numerals *I, II, III*; the leaves by a_I, b_I, etc. a_{II}, b_{II}, etc.; C_I has been cut off. *B*. The upper part of a plant with a flower (about $^2/_1$). *C*, shows a young nutating leaf the sheath of which surrounds the apex of the shoot (about $^1/_1$).

a somewhat downward tendency, always shorter than those which proceeded from the lower leaves. The uppermost leaf may also subtend a floral-axis which bears a leaf without axillary flower. Adventitious roots arise within the nodes of the shoot during the first summer but as a rule they probably do not emerge until the next summer, when the shoot flowers (Fig. 46). It is not probable that the individual shoot-generations live more than two summers. The plant probably passes the winter in a similar manner to *R. hyperboreus*.

The different parts of the plant are often very long; thus the internodes, fruit-stalks and leaf-stalks measured as much as 14 cm.

Andersson & Hessselman (l. c.) have proved that the var. *Spitzbergensis,* established by Nathorst (l. c.), is a hybrid between *R. lapponicus* and the present species; it is the only hybrid known from Spitzbergen. In regard to the majority of the characters of this variety it is intermediate between the two parents, and Andersson & Hesselman have a long series of statements concerning such characters, as, for example, comparisons of the leaves, the lower ones of which in *R. Pallasii* are usually tripartite and the upper ones entire and lanceolate, while in the hybrid they are relatively broader and 5 or 3-partite. Again in *R. Pall.* the lamina almost continues the direction of the stalk; in *R. lapp.* it stands at an angle with the stalk; while the hybrid is intermediate in this respect.

The flower has three perigone-leaves; in *R. Pallasii* it has 7, or sometimes 6—8 white nectary-leaves, but in the hybrid there are usually 6 greenish-yellow nectary-leaves. The nectary-leaves are somewhat longer than the perigone-leaves. The diameter of the flower is usually 15 mm. in *R. Pallasii* and somewhat smaller in the hybrid. The nectaries are simple and pocket-shaped (Fig. 47, *A*). The flower in both has a strong perfume, according to Nathorst that of *R. Pallasii* is reminiscent of *Platanthera.* The flowers are proterogynous-homogamous in *R. Pallasii* according to Ekstam who has observed the visit of small Diptera. The carpels in *R. Pallasii* have an almost straight beak, the hybrid is intermediate in this respect between *R. Pallasii* and *R. lapponicus* with its markedly bent beak.

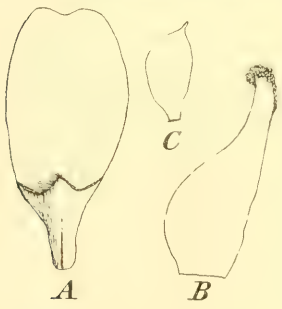

Fig. 47. *R. Pallasii.*

A. Nectary-leaf (4/1). *B.* Carpel (11. 8. 1882; 9/1). *C.* Almost ripe fruit (Siberia; 18. 6. 1876; Herbarium-material; 3/1).

Flowering takes place in the middle and the end of summer; in Spitzbergen ripe fruit has not been observed (Ekstam, Nathorst); but it can certainly be developed in Siberia (Fig. 47, *C*). — *R. Pallasii* and the hybrid both grow in moss.

Geographical Distribution. The hybrid has been found in Spitzbergen only; *R. Pallasii* in Arctic America and Labrador, Spitzbergen, Arctic Finland, Arctic Russia, Nova Zembla and North Siberia (Nathorst).

Anatomy. The roots are often very long, filiform, and usually unbranched. Their structure is of the common type and the texture is exceedingly loose. The epidermis and the exodermis were suberized, the latter had undulating walls. A few layers of the cortex remained within the exodermis and a few outside the endodermis, also some slender, radiating trabeculæ. The endodermis was suberized, the walls were not thickened. The central cylinder was diarch. A few thin-walled root-hairs occurred. The starch-grains are compound, especially in the inner layers of the cortex. — I did not find hyphæ in the roots.

In *R. Pallasii* the internodes of the horizontal stem and the peduncle (in the flowering period) had a similar structure. The cortex was few-layered and had numerous large intercellular spaces (Fig. 48, *C*). The epidermis showed a slightly striped and indistinct cuticle, and the outer walls of its cells were thin; the latter contained some chlorophyll. The stomata were on a level with the surface. From seven to eight vascular bundles occurred; in the peduncle they were surrounded by a somewhat greater amount of close-set parenchyma than in the internodes of the stolon. The specimens examined contained neither bast nor lignified parenchyma, but perhaps these are developed in the peduncle during the ripening of the fruit when it stands stiffly erect (herbarium-material). The bundles are arranged very excentrically in the thick stem, and the whole of the pith is broken down (Fig. 48, *B*).

The nodes of the stem resemble in structure those of *R. lapponicus*. The roots no doubt remain a long time within the epidermis of the parent-rhizome; they showed distinctly plerome, periblem and dermocalyptrogen. (Fig. 48, *A*).

R. Pallasii and *R. lapponicus* differ in the structure of their peduncles (see Fig. 43); also in this point the hybrid is intermediate; the young plant in the flowering stage which I investigated had no interfascicular stereom, but a weak fibrous tissue outside the leptome; upon the inner side of the bundles the endodermis was lignified.

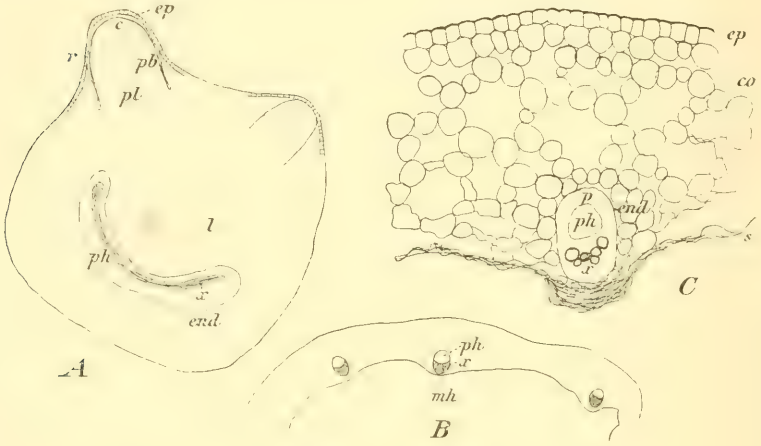

Fig. 48. *R. Pallasii.*

A. Transverse section of a node of a stolon (17/1). *B*. Portion of transverse section of stolon (17/1). *C*. Piece of the same (75/1); *ep*, epidermis; *c*, calyptra; *co*, cortex; *r*, young root; *pb*, periblem; *pl*, plerome; *ph*, leptome; *x*, xylem; *l*, lacuna; *p*, non-lignified parenchyma; *s*, collapsed tissue; *mh*, pith-cavity.

The leaf is glabrous in *R. Pallasii* and somewhat fleshy; the thickness varied between 340 and 510 μ. It has brown spots especially upon the upper surface, as the epidermal cells probably contain tannin as in *R. lapponicus* (see p. 403); the epidermis also contained chlorophyll and the outer walls of its cells were about 3 μ thick; the radial walls were somewhat undulating, almost equally upon both surfaces. The stomata were on a level with the surface or projected slightly, about

50 were found per sq. mm. upon both surfaces; they were somewhat unevenly distributed. Cells containing tannin occurred to the number of about 35 per sq. mm. upon the upper surface, and were also unevenly distributed; upon the lower surface only a few occurred.

The leaves of *R. Pallasii* which were investigated had two

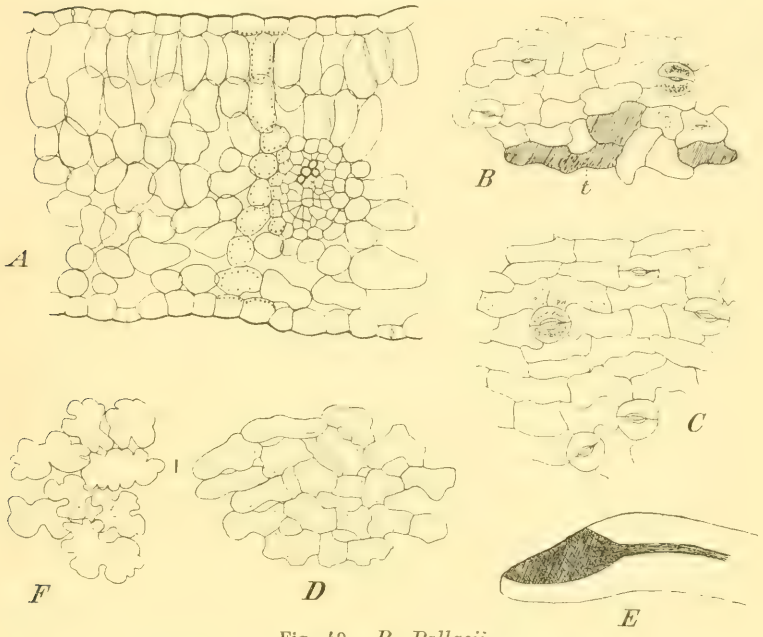

Fig. 49. *R. Pallasii.*

A, Transverse section of leaf (100/1). *B*, Epidermis of the upper surface of the leaf (85/1); *t*, cells the contents of which are probably tannin. *C*, Epidermis of the lower surface of the leaf (85/1). *D*, Surface section of spongy tissue (55/1). *E*, Longitudinal section through the leaf-apex, showing the position of the epithema (17/1). *F*, Cells of the epithema with *nuclei* (220/1).

palisade-layers which constituted from $^1/_2$ to $^1/_3$ of the thickness of the mesophyll; the individual palisade-cells were irregular, about twice as long as they were thick, and only slightly inclined towards the leaf-apex. There was a gradual transition to the spongy parenchyma; the cells of the latter were shortly branched or stellate, and as usual, those of the subepidermal

layer more strongly so than the rest. (Fig. 49). The bundles were found to be surrounded by a sheath containing chlorophyll; stereom was absent; the palisade-layers continued unaltered across them.

At the leaf-apices an extensive epithema was found, consisting, as in the other species, of shortly branched cells with undulating walls. The water-pores open upon an oblique, upwardly-directed surface upon the leaf-apex (Fig. 49, *E*, *F*).

The transverse section of the leaf of the hybrid is figured by Andersson & Hesselman together with that of the leaf of the parents; also in this point the hybrid is intermediate.

The leaf-stalk of *R. Pallasii* closely resembles the stem in structure and the transverse section is almost circular in outline.

Batrachium confervoides Fr.

Synonyms: *B. paucistamineum δ. eradicatum* (Læst.). *R. aquatilis* v. *eradicata* (Læst.). *R.* paucistam. *δ*, *confervoides* Tullb. *R. paucistam.* v. *borealis* Beurl.

Lit. Gelert, 1894, p. 28. Norman, 1895, p. 33. Rosenvinge, (III), 1896, p. 240. Kruuse, 1897, p. 385. Dusén, 1901, p. 29. Porsild, 1902, p. 206.

Alcohol material from Greenland (Sophiehavn 5. 6. 8. 1883), Iceland, (Nallanes, 10. 1. 1894).

This species is like the majority of the species of *Batrachium* a perennial, herbaceous water-plant with branching stems which creep upon the mud at the bottom of the water and send up to the surface in the spring long, filiform, branching shoots. *Batr. confervoides* has only finely-divided, stalked leaves, arranged in a $^2/_5$ spiral; the shoot becomes sympodial when flowering begins. The peduncles are of the same length as the leaves; they bend backwards during fruit-setting. Long, slender, adventitious roots, unbranched in places, arise from the nodes of the erect shoots.

The flower has five perigone-leaves and five white nectary-leaves which are about twice as long as the perigone-leaves; the nectary-leaves have a yellow claw, and bear a tubular cornet-shaped nectary (Fig. 50, *A*). There are 6—10 stamens, which are longer than the head of carpels. The fruits are wrinkled and hairy, and almost without a beak. Of the flower-buds, in the material from Iceland (Jan. 10) which has been investigated, the lower and older ones had partially-barren stamens, while no such stamens were observed in the upper buds. The diameter of the flower is 3—5 mm. (Greenland). As far as I know, no observations on the flower-biology of the species have been published, but as other species in the genus it is probably homogamous.

The flowering period in Arctic Norway is from the beginning of July to the middle of September, and ripe fruit was observed in the middle of August (Norman).

The fruit is probably dispersed by the agency of the water (cf. Kølpin Ravn, Bot. Tidsskr., XIX).

The fruits of other species of *Batrachium* are capable of germinating during the year in which they ripen (Gelert, Sylvén, 1906, p. 279), and in Scandinavia the seedlings pass the winter in a green condition.

Batr. confervoides grows, by preference, in small pools and in rills, no doubt usually in shallow water; but Kruuse (l. c.) found it at Egedesminde in West Greenland growing in a depth of as much as 3 m., and found that it sets fruit but rarely in water shallower than 1·5 m. Porsild (l. c.) saw it in Disco in water not shallower than 30 cm. and especially in the neighbourhood of large boulders and then always upon the side most exposed to wind and water. In Arctic Norway it does not appear to regard the temperature of the water, as it sets ripe fruit both in streams with affluents from snowy mountains and also in water with a relatively high temperature (Norman).

It can survive getting dry during summer (Rosenvinge, Norman); in such cases its leaf-segments become oval in transverse section.

This species appears to occur especially frequently in Greenland, Iceland, northern Scandinavia and Finland (Gelert).

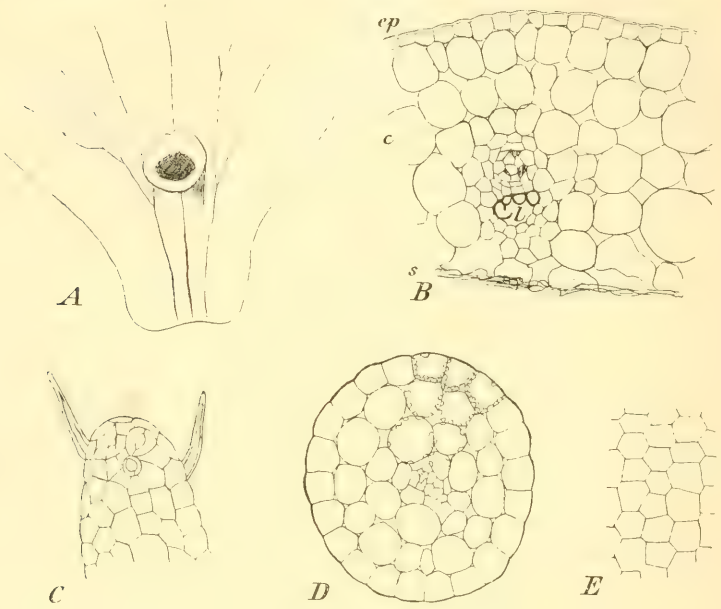

Fig 50. *Batrachium confervoides.*

A, Base of nectary-leaf with nectary (Greenland; $^{12}/_{1}$). *B*, Portion of the transverse section of a stem (Iceland; $^{120}/_{1}$). *ep*, Epidermis; *c*, cortex; *l*, lacuna; *s*, collapsed tissue. *C*, Apex of leaf with hair and water-stomata (Iceland; $^{140}/_{1}$). *D*, Transverse section of segment of an aquatic leaf (Iceland; $^{170}/_{1}$). *E*, The epidermis of an aquatic leaf (Iceland; $^{120}/_{1}$).

Anatomy. The adventitious roots which arise upon the ascending stems resemble in structure those of the examined species of *Ranunculus*. The epidermis and the exodermis are suberized; the former shows a tendency to collapse, the latter has slightly-undulating radial walls. The greater part of the coxtex breaks down at an early stage. The endodermis is suberized. The central cylinder is diarch; the woody masses are not in contact with each other. — Mycorrhiza was absent.

I have only had material of ascending stems for investigation. With the exception of some small modifications their structure resembles that of the examined species of *Ranunculus*. The cells of the epidermis are much smaller than those of the cortex; as many as seven layers of the latter occur and they are somewhat more closely placed than are the cortical cells in those species of *Ranunculus* which have been investigated (Fig. 50, *B*). The 3—5 bundles are each surrounded by an endodermis which is slightly lignified in the older stems. As is also the case in other species of *Batrachium* the woody mass in the bundle frequently encloses a large air-space, produced by the breaking down of young vessels; remnants of the walls are often seen projecting into the space. In the material from Iceland (January) these canals had just begun to develop in a young internode which was nearly one cm. long. The continuous pith-cavity which occurs in full-grown stems had not yet begun to develop in the internode in question.

The leaves resemble in structure the divided leaves of other species of *Batrachium*; the segments of the aquatic leaves are cylindrical with an axial bundle surrounded on all sides by a few layers of homogeneous, elongated non-prosenchymatous cells (Fig. 50, *D*). The epidermis contains a larger quantity of chlorophyll than the inner layers; the radial walls of its cells are straight. Only one or two stomata occur at the apex of the segments (Fig. 50, *C*); they resemble in form the water-stomata figured for *R. nivalis*. The apex of the leaf usually bears 1—4 hairs; but sometimes these are absent.

When the plant becomes dry during summer (cf. Rosenvinge) it develops, in common with other species of *Batrachium*, leaves which in form and certainly in internal structure differ from those of the aquatic form (cf. Askenasy, Bot. Zeitung, 1870). Such leaves were not found upon the Arctic specimens which I have had for investigation; but a land-form of the nearly-

related *Batr. paucistamineum* (Tausch) Gelert, from Denmark, exhibited the following structure: The leaf-segments had become oval in transverse section; there was only one bundle, but the tissue on its upper side and partly also beside it had developed into 1—2 palisade-layers, of which some individual cells were about twice as long as they were thick; upon the under side of the bundle the cells were more like those of the aquatic leaf. Moreover, intercellular spaces were more abundantly present in the mesophyll than in that of the aquatic leaves. The radial walls of the epidermis were undulating and the upper surface had as many as 80 stomata per sq. mm. while many fewer (about 10 per sq. mm.) occurred upon the lower surface. The Danish land-form had retained some chlorophyll in its epidermis. The land-form had retained the water-pores at the apex of the leaves.

Anemone Richardsoni Hook.

Lit. Hooker, 1833. Lange, 1887. Janczewski, 1898, p. 507.

Alcohol material from Præstefjæld (Holstenborg), West Greenland, 1884, and 4.8.1886.

This species, like *A. nemorosa*, is a perennial herb with a horizontally elongated rhizome which becomes sympodial when flowering begins. The principal bud is subtended by the last leaf (Fig. 51, *A*). The rhizome may become very long (20 cm.), and the length of the internodes is usually 1—3 cm.; they are about 1·5 mm. thick. The present species differs from *A. nemorosa* not only in regard to the rhizome but also as regards the leaves, the majority of them being foliage-leaves; Janczewski writes "all" but a specimen in the herbarium shows one scale-leaf distinctly. The rhizome can produce at least four foliage-leaves during one summer; they are long-stalked and the lamina is deeply 3-lobed with ovate, deeply-indented segments.

The principal bud may produce leaves during the first year, but I do not think it does so always, the first leaf is placed laterally in reference to the subtending leaf; the bud in question may attain the flowering stage the same year as the parent-axis. In the herbarium-specimens, the second flowering

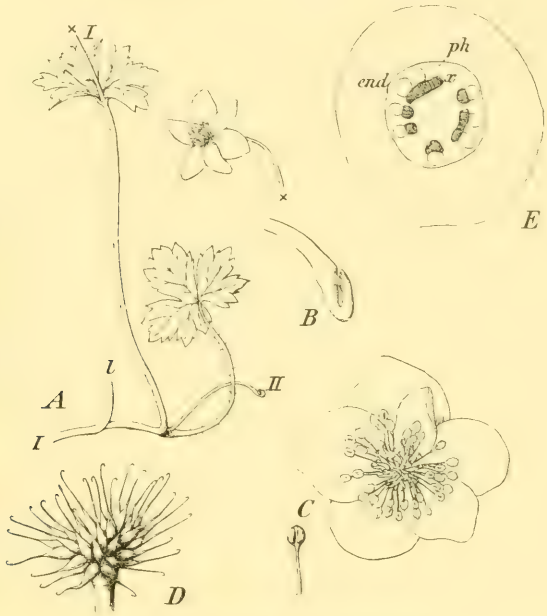

Fig. 51. *Anemone Richardsoni.*

A, A fragment of a plant from Præstefjæld; 16. 7. 1884; 1/2. The flower has been cut off and placed by the side. The upper foliage-leaf subtends the principal bud of which the growth begins with an elongated internode; *l*, basal part of the stalk of a foliage-leaf. *B*, The apex of a rhizome with a nutating leaf, the sheath of which surrounds the tip of the shoot (5/2). *C*, Flower seen from above (3/2). The perianth leaves are of unequal size; a stamen is placed by the side of the flower (5/2). The anthers are turned inwards. *D*, Cluster of fruits, almost ripe (2/1). *E*, Transverse section of rhizome (17/1); *end*, endodermis; *ph*, leptome; *x*, xylem (*A*, *B*, *C*, *D* were drawn by E. Warming).

axis on such individuals had a foliage-leaf which subtended the rejuvenating shoot. Also other leaves than the uppermost one may subtend shoots which are very similar to the principal bud. — The slender, branched, adventitious roots arise from the rhizome a short distance below each node.

The erect peduncle attains a height of from 5 to 20 cm. and bears a tripartite involucre which, when flowering begins, is seated above the middle of the peduncle, but is considerably below that point when the fruits are ripe, the upper part of the axis having elongated greatly. The peduncle is somewhat hairy, the hairs being most dense upon the upper part.

The flower has $3 + 3$ yellow perianth-leaves, sometimes $4 + 4$, and the leaves in the whorl are of unequal size (Fig. 51, *C*). In the expanded flower the filaments are bent outwards towards the perianth-leaves, the anthers are introrse. At first the long backwardly-turned styles are erect, but afterwards, they probably become so far turned outwards that they can reach the anthers. The diameter of the flower is 19—22 mm. Honey is absent. (Warming, notebook).

Flowering begins at the end of June and is continued into August. The fruits may certainly be dispersed epizoically, as the styles of the carpels are long (about 4 mm.) and hooked at the apex (Fig. 51, *D*).

In Greenland it has been found only at Holstensborg and Sukkertoppen; it grows there in damp places in willow copses. It is morever found in arctic and subarctic America from Hudson's Bay to Alaska, Rocky Mountains, Unalaschka, East Siberia (Lange).

Anatomy. The roots are slender and branching; they remain in the primary condition. In their anatomy they greatly resemble those of *A. nemorosa*. The epidermis is suberized; its outer wall is fairly thick, and highly convex. The cortex is 5-layered and compact in structure with very small intercellular spaces, the walls of the cells are fairly thick. The starch-grains in the cells are both single and compound. The cells of the endodermis are tangentially elongated, the walls are somewhat thickened and are corky: the pericycle is one-layered. The central cylinder is diarch, in the larger roots the woody parts meet in the middle. In the more slender roots the epidermis is collapsed.

Mycorrhizas are present; the hyphæ form balls in the inner cortical cells.

The rhizome (Fig. 51, *E*) is rounded, and in its anatomy bears resemblance to that of *A. nemorosa*, but it is not so decidedly modified to contain reserve food-material. The epidermis is not especially thick-walled; the cortex is compact in structure, the intercellular spaces are not large. Concentric with the epidermis and about midway between it and the centre of the rhizome is an endodermis which when young shows Caspary's dots. From five to ten bundles are arranged in a ring; the woody parts which have large vessels are often more or less fused together. Their number then may be ascertained from the leptome-groups, which occur isolated from each other. The pith is not broken down. The starch-grains are highly compound.

The peduncle has about 12 bundles which in the young stalk are devoid of stereom, but in the older fruit-stalk, have about four layers of fibrous tissue outside the leptome and a fairly definite, interfascicular lignified ring of about five layers with somewhat thickened walls. Between the vessels and the sieve-tissue a little wood-parenchyma is found and on the inner side of vessels occurs a considerable amount of small-celled, slightly collenchymatously thickened parenchyma, which is bounded internally by an endodermis-like layer which abuts upon the somewhat large-celled and more or less broken-down pith. — The cortex consists of 6—7 layers and is looser in structure than that of the rhizome; in the outer part there are tangential schizogenous lacunæ. The cells of the epidermis have but slightly thickened outer walls and a smooth cuticle; they contain some chlorophyll. The stomata are on a level with the surface or else project slightly; the hairs are unicellular, slightly suberized and often excentrically thickened.

The leaf is slightly hairy along the margin and bears, scattered on both surfaces, pointed hairs the walls of which

are thickened; there occur in addition small club-shaped, thin-walled hairs, rich in contents, but far fewer in number (compare *R. acer*) (Fig. 52, *B*). The cells of the epidermis contain some chlorophyll and have undulating radial walls, which are however more or less straight above the larger nerves. Only very few stomata occur upon the upper surface, but upon the lower surface there are, on an average, about 40 per sq. mm., either

Fig. 52. *Anemone Richardsoni.*

A, Transverse section of leaf. *B*, The epidermis of the upper surface with a club-shaped hair. *C*, The epidermis of the lower surface. *D*, Surface section of palisade-cells. *E*, Surface section of spongy parenchyma. *F*, Longitudinal section through the apex of a leaf; *l*, a lacuna between the epidermis and the epithema; some tracheids are seen, *tr*. (*A*, *B*, *C*, *D*, *E*, $^{105}/_{1}$; *F* $^{90}/_{1}$).

on a level with the surface or slightly projecting; they are not evenly distributed and the apertures do not lie in any fixed direction. The palisade-layers constitute only a small part of the mesophyll, the majority of their cells have incomplete walls (Fig. 52, *A*). The spongy parenchyma consists of abundantly branching cells and is very loose in structure. The bundles are surrounded by a sheath containing chlorophyll, and the larger ones have conducting-parenchyma upon their upper and lower surface.

The larger teeth of the leaf contain an epithema which

opens almost at the margin and of which the cells have undulating walls (Fig 52, *F*).

The leaf-stalk is hairy like the peduncle. The epidermis contains chlorophyll and is thin-walled. The cortex has numerous tangential schizogenous lacunæ. There are three bundles which upon the outer side have about three layers of fibrous tissue; their structure is otherwise almost entirely like that of the bundles of the flower-stalk. Interfascicular stereom is absent. The pith is more or less broken down.

Thalictrum alpinum L.

Lit. Lecoyer, 1878, p. 9, pl. III, fig. 28. Lindman, 1887, pp. 18, 44, 101. Lange, 1888, p. 53. Rosenvinge, (I), 1892, p. 675. Borgesen, 1895, pp. 236, 37, fr. res. p. 7. Hartz, 1895, (II), p. 289. Norman, 1895, p. 37. Ekstam, 1897, p. 148. Cleve, 1901, p. 50. Dusén, 1901, p. 29. Skottsberg, 1901, p. 16. Freidenfelt, 1904, pp. 49, 50, pl. III, fig. 38.

Alcohol material from Sweden (Jemteland, 6. 8. 1881); the Færöes (Kirkebö); Iceland (Havnefjord, 4. 7. 1894, unknown loc., 15. 5.); Greenland (Kobbefjord, 29. 6. 1884, Godhavn, 26. 7. 1884).

This plant, as also *Coptis trifolia*, has a subterranean rhizome which is horizontal or somewhat slanting, is slender, has elongated internodes and bears scale-leaves in a spiral. This rhizome will afterwards bend upwards with its apex; its internodes will become short; it will pass the winter with a bud covered with scale-leaves which will next spring produce one or several long-stalked foliage-leaves. Perhaps the axis may develop further and produce an inflorescence. The flowering axis often bears halfway up a short-stalked foliage-leaf of the same nature as the basal leaves. Small oval bracts subtend the flowers in the racemose inflorescence (Fig. 53, *A*). The principal bud occurs in the axil of one of the basal leaves, and the structure of the shoots is consequently sympodial. The majority of the flowering

individuals in the alcohol material examined by me had only basal leaves and short internodes in the rosette of the leaves, of these the one next below the uppermost subtended the principal bud. The subtending leaf was either a scale-leaf or a foliage-leaf with a large sheath. Upon the other flowering individuals the uppermost basal-leaf was preceded by a somewhat elongated internode. Perhaps the principal bud is really subtended by the uppermost basal leaf upon individuals whose aerial stem bears a median foliage-leaf; this leaf may subtend an inflorescence similar to that of the parent-axis.

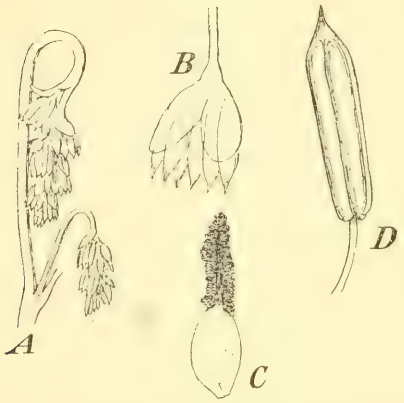

Fig. 53. *Thalictrum alpinum.*
A, Young inflorescence (Kobbefjord; 29.6.1884; about $^{3}/_{1}$). *B*, Flower which has not yet expanded (ibidem; about $^{10}/_{1}$). *C*, Carpel from expanded flower (Jemteland: June. 1881; about $^{12}/_{1}$). *D*, Stamen (Kobbefjord; 29.6.1884; about $^{20}/_{1}$). (*A*, *B* and *D* were drawn by E. Warming).

The rejuvenating shoot develops a rosette of foliage-leaves during the same year as that in which the parent-axis flowers, and produces during autumn a winter-bud protected by scale-leaves. The leaves are long-stalked and pinnate or bipinnate, with opposite, stalked primary segments, and broadly ovate, glistening, glabrous leaflets that are bluish-green upon the lower surface and of which the edges are revolute.

The vertical part of the rhizome, may, in addition to the principal bud, also produce other ascending rosette-shoots and scale-bearing rhizomes; some however are met with that bear foliage-leaves upon elongated internodes, probably due to the fact that the rhizome has been lying close to the surface. The horizontal rhizome may give off branches. From the vertical rhizome arise strong, brown, branching roots, the cortex of which is wrinkled and rough on account of the secondary growth;

from the horizontal part of the rhizome only slender roots arise.

The numerous stamens protrude far beyond the four closely placed, delicate perianth-leaves (Fig. 53, *B*), the colour of which varies somewhat from yellow to violet or greyish-red to grey-green. The stamens have usually violet filaments and brownish-yellow anthers.

Axell (1869) found *Thalictrum alpinum* to be homogamous, Lindman and Ekstam (l. c.) protogynous-homogamous. Lindman thinks that it is especially during the homogamous stage that the stigmas receive pollen, as they are covered by the far-protruding stamens and the bell-shaped perianth. Warming (notebook) found no honey in Greenland specimens. No pollinating agents have been observed; the plant is anemophilous (Lindman, Warming, notebook).

Lecoyer figures anthers of *Thalict. alp.* from the different habitats of the plant and finds great variation in their length as well as in that of the elongation of the connective of the anther; for instance, according to him, there is a great difference between the anthers from Norway and those from Lapland. In the material at my disposal they all resembled the one which I have figured from Kobbefjord in Greenland (Fig. 53, *D*); in specimens from Arctic Russia the stamens were however somewhat smaller and the connective was somewhat longer and more pointed.

Thalict. alpinum flowers in July and the fruit ripens in August. Lindman (l. c. p. 101) found fruit with seed capable of germination at a height of 900 m. — The fruit is dispersed by the agency of the wind, according to Ekstam (1897).

In Arctic Norway *Thalictrum alpinum* is found both in the lowlands and the highlands, on horizontal ground and on slopes; it is about twice as common upon the sunny side as upon the indifferent and shady sides; it can grow in pools and can live

with plants which overshadow it (Norman). In Nova Zembla it grows upon dry slopes (Ekstam).

Geographical Distribution. Arctic America, East and West Greenland, Iceland, the Færöes, Scandinavia, Finland, the Alps, Caucasus, Arctic Russia, Nova Zembla, North Siberia, Altai and Asiatic coast of Bering Strait.

Anatomy. The adventitious roots of the first order. The primary cortex is thrown off or else persists as dead layers around the secondary formation. In a young root from Iceland, gathered in May, tangential lacunæ had been developed between the endodermis and the primary cortex, the outer layer of which was somewhat collenchymatously thickened, while the epidermis was thin-walled and corky. The secondary cortex resembled the primary in the fact of its outer layers being also somewhat collenchymatous; the inner layers were thin-walled and distinctly radially arranged. The thin-walled endodermis had replaced the primary epidermis; its cells were tangentially elongated. The central cylinder is triarch or tetrach or according to Marié, even pentarch or hexarch; the secondary vessels were larger than the few primary ones. The cambium was complete.

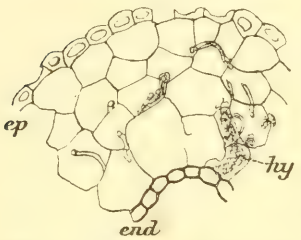

Fig. 54. *Thalictrum alpinum.* Fragment of transverse section of root of second order (Iceland: Havnefjord; $^{45}/_{1}$). *ep*, Epidermis; *hy*, hyphæ; *end*, endodermis.

The roots of the second order remain in the primary condition and are diarch. The endodermis is slightly thickened. The cortex consists of four thin-walled layers, of which the innermost is the largest. The epidermis is remarkable owing to the fact that it is dimorphic (Fig 54); it is partly of thin-walled cells which collapse at an early period, and partly of cells of which the walls thicken at an early period (Freidenfelt). These roots contain spongy hyphæ.

The rhizome, also, has secondary growth. The youngest

stage of a horizontal one which I observed had from one to a few vessels in the eight masses of wood, and an incomplete ring of sclerenchyma, no doubt outside and also including the endodermis, but the latter was not distinct. A later stage showed the ring of sclerenchyma 1—3 layers thick, in a complete condition; still later, the thin-walled primary cortex, 5—6 layers thick, was found to be collapsed, and in the full-grown stage it had been thrown off together with the sclerenchyma-layer. The epidermis is one-layered and thin-walled. The secondary cortex has on the outside some layers of dead, suberized cells, and within these a somewhat collenchymatously thickened part; the innermost part is thin-walled and the cells are arranged radially.

The wood-masses are either fused together or are separated by narrow medullary rays from which cambium is absent; otherwise the latter is complete. The cells of the pith are thin-walled and more or less collapsed in the older rhizomes. The structure of the vertical part of the rhizome was similar to that of the horizontal part, only it was thicker, the course of the bundles was irregular and thin-walled parenchyma was more abundant among the secondary vessels.

The peduncle is short and thick and pentagonal. The epidermis is fairly thick and contains chlorophyll; the cuticle is smooth, and the stomata are on a level with the surface. The cortex is 5—6 layered and consists of fairly closely placed cylindrical cells; intercellular spaces are absent between the subepidermal layer and the epidermis. In the outermost layers in the angles of the peduncle, only very little or no collenchyma occurs; such a tissue is found in other species of *Thalictrum*. Outside the 7—10 bundles there is a ring of bast which, opposite to the bundles, is as much as 7 layers thick while in the interfascicular part about three layers are found: the sieve-tissue occurs close to the bast-layer; in the adult peduncle no endodermis was to be seen; the cambium is

rudimentary. On the inner side of the vessels, which are arranged as a V or in 2 lateral masses separated by thin-walled parenchyma, some small-celled parenchyma occurs, easily distinguishable from the large-celled pith; the latter was broken down in the older stems, leaving a pith-cavity.

The leaf is less hydrophilous in structure than are those of the previous species. Hairs are absent. The epidermis of the upper surface is about 28 μ thick, while that of the lower surface is about 17 μ, and it is almost entirely devoid of stomata; its radial walls are somewhat undulating, and the cells are homogeneous. The cells of the lower surface, on the other hand, vary more in form; most frequently the radial walls are undulating, almost like those of the upper surface, but they may also resemble those shown in Fig. 55. *C*, and the difference does not appear to have any connection with the number of the stomata; the number varies greatly, and numbers between 280 and 420 per sq. mm. are the most common. The stomata are on a level with the surface; their direction is not fixed; they occur only between the larger veins and not above them. The epidermis contains a little chlorophyll. The radials walls of the lower surface are furnished with pores.

The bundles are situated nearer to the lower surface, the larger ones, both upon the upper and lower surface, are accompanied by stereom which extends to the epidermis of both surfaces; the smaller bundles either have a little bast upon their under sides or are only provided with a sheath in which chlorophyll occurs, especially along the outer walls.

The palisade-cells are in 2—3 compact layers which constitute about $^1/_2$ or $^2/_3$ of the mesophyll; the quota of the palisade-cells is about $^1/_3$; there is a somewhat abrupt transition from the palisade to the spongy parenchyma, the rather small cells of which were somewhat branched and loosely connected (Fig. 55 *A*, *D*).

The specimens from Iceland differed somewhat from the

others which were investigated, in that the leaves were somewhat less thick (about 210 μ against about 280 μ from Greenland and Scandinavia) and there were only two palisade-layers, while those from Greenland and Scandinavia had three layers. The leaves from the Færöes, which have been investigated, resembled those from Iceland.

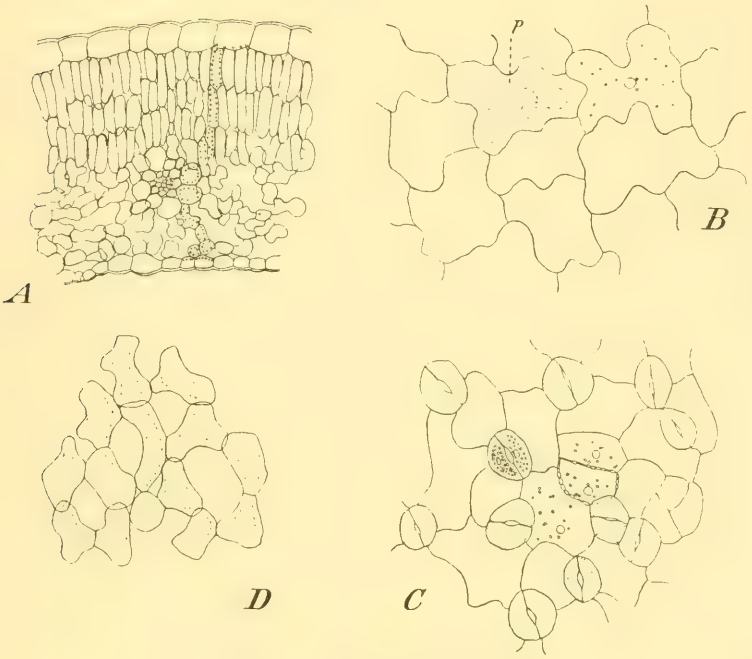

Fig. 55. *Thalictrum alpinum.*

A, Transverse section of leaf (Godhavn; $^{90}/_{1}$). *B*, Epidermis of the upper surface (Havnefjord; $^{230}/_{1}$); *p*, palisade-cells. *C*, Epidermis of the lower surface; (Godhavn; $^{230}/_{1}$); the perforation of the wall has been drawn only in one cell. *D*, Surface section of spongy parenchyma (Godhavn; $^{230}/_{1}$).

The leaf-stalk is obtusely square in transverse section. The ring of sclerenchyma and the four large and four small bundles resemble in structure the corresponding parts of the stem. The epidermis contains chlorophyll and the cuticle is slightly striped. The cortex consists of 4—6 layers. The pith is large-celled and not broken down.

All the specimens which have been investigated from the different districts, with the above-mentioned exceptions, were found similar in structure.

Coptis trifolia Salisb.

Lit. Hooker, 1833. Marié, 1885, pp. 103—105. Lange, 1887. Maxwell, 1893, p. 100. Rosenvinge, (I), 1892, p. 677; (II), 1896, p. 67.

Alcohol material from Greenland (Julianehaab, 20.6.1883, Nuluk 23.6.1883, Friedrichsthal, 29.8.1883, Kobbefjord, 28.6.1884, Sukkertoppen, 16.8.1884, and 15.7.1895, Godthaab, 20.7.1895, Frederikshaab, 8.7.1892).

Coptis trifolia is a perennial herb with subterranean, horizontal rhizome and evergreen leaves. The horizontal rhizome is yellow and slender, has elongated internodes and bears scale-leaves arranged in a spiral. The length of an internode is about one cm., and the rhizome may attain to a considerable length (about 20 cm.). The scale-leaves often subtend lateral shoots of the same kind as the parent-axis. The slender, branched roots arise especially from the nodes. After the horizontal rhizome has developed scale-leaves for some time, it produces short internodes and foliage-leaves and the axis becomes an ascending one. After this, foliage-leaves alternate with scale-leaves so that the first leaves which the shoot develops in the summer are foliage-leaves (probably at most four) and the next scale-leaves also separated by short internodes; the scale-leaves protect the bud which remains throughout the winter, and the next spring the bud recommences the growth with foliage-leaves, etc. The usually solitary flower is terminal upon a penduncle which bears a bract; sometimes the bract subtends a flower. I have found the length of the peduncle to be from 2 to 12 cm.; it is scarcely probable that it grows much during the time of fruit-setting.

The uppermost scale-leaf subtends the principal bud

Fig. 56), but other scale-leaves may also subtend shoots. The first leaves upon the shoots are foliage-leaves, and they develop during the same year as the flower of the parent-axis; the first two are lateral, while the others (foliage-leaves and scale-leaves) follow in a spiral, those scale-leaves which develop last protecting the bud for the next year. The principal bud frequently flowers the same year as the parent-axis, and in

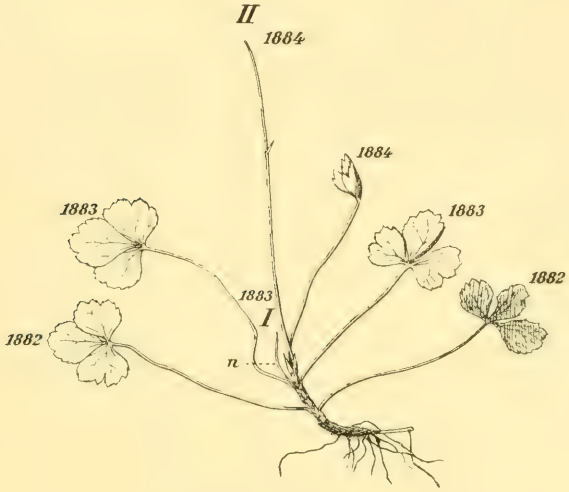

Fig. 56. *Coptis trifolia.*

(Sukkertoppen; 10. 8. 84 1/2). The two lowermost leaves were developed in 1882, after which scale-leaves were developed; the shoot I flowered in 1883; the uppermost scale-leaf on axis I subtended axis II, of which the foliage-leaves were developed in 1883; the shoot flowered in 1884, and the first leaf of the principal bud developed in the same year.

that case its uppermost scale-leaf subtends the bud which remains throughout the winter, and which by that time may have developed about three foliage-leaves.

The scale-leaves are leaf-sheaths morphologically, the upper ones often bear small, rudimentary laminæ. The foliage-leaves have a short, compact sheath, a long and slender stalk, and a tripartite lamina with broadly ovate segments that are shallowly lobed and have pointed teeth. The bracts are either lanceolate sheaths, and are in such a case no doubt colourless,

or they have a small tripartite laminæ and then doubtless contain chlorophyll.

The flower has 5—7 lanceolate, stellate, expanded, white perigone-leaves and a varying, but smaller, number of spoon-like orange-coloured nectaries often thickened at the apices and sides; transitional forms between the short, spoon-like and the ordinary leaf-form are often met with (Fig. 57). The anthers are numerous with thin filaments; the carpels are 6—10 in number, are long-stalked at maturation, and the style is hooked, at any rate in the half-ripe fruit. The spoon-like nectaries according to Warming (notebook) drip with honey. The diameter of the flower is from 0·6 to 1 cm. The flowers investigated were rather markedly protogynous. In the scarcely-expanded flower the filaments are short and erect and the anthers are still closed, while the papillæ upon the tall carpels begin to develop in basipetal succession; gradually the filaments elongate and bend outwards, then the laterally-turned anthers open, but even the elongated stamens can scarcely reach the stigmas. Lastly, a homogamous stage occurs. This description is based upon the spirit material exclusively.

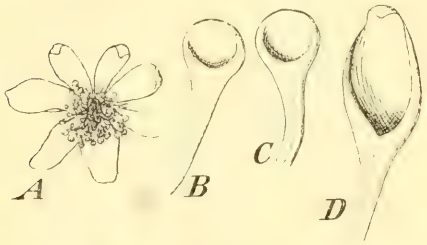

Fig. 57. *Coptis trifolia.*
A, Flower from Nuluk in Greenland, drawn at the end of the ♀ stage (about $^2/_1$). *B, C*. Two common forms of nectary-leaves. *D*, Nectary-leaf with more common leaf-form. *B. C* and *D* from Sukkertoppen in Greenland ($^{10}/_1$).

The flower begins to develop in May; the fruit ripens probably in August. In South Greenland *Coptis trifolia* sets ripe fruit (Warming), and Rosenvinge (II l. c.) records it with flowers and with fruit of the previous year, at the end of July, from N. Strømfjord, which is its northern limit in Greenland (67° 32′ N. lat.). The seed is probably dispersed by the agency of the wind, or perhaps it is also epizoic.

In Greenland the habitats are grassy slopes, copses and luxuriant heaths (Rosenvinge, (I).

Geographical Distribution. West Greenland (common south of Godthaab), Labrador, Canada, Unalaschka, Kamtchatka, Arctic Siberia (Lange, Rosenvinge, (I).

Anatomy. (Compare Marié l. c.). The epidermis of the root of the first order is more or less collapsed and corky and bears root-hairs; the exodermis has somewhat thickened walls in which the middle lamella is suberized. The cortex is from 4 to 6 layers thick, the cells are somewhat collenchymatous and the intercellular spaces very small. The endodermis has somewhat thickened, suberized walls; the pericycle is one-layered. The central cylinder is diarch, the vessels filling up the greater part of it; the two groups of sieve-tissue are diametrically opposed to each other and are surrounded by wood-vessels upon the three sides. In the roots of the second order the cortex consists of about three layers; the innermost layer is of large, radially elongated cells, the outermost has somewhat collenchymatously thickened walls. The epidermis has a tendency to collapse, it may however bear numerous root-hairs. The groups of wood in the diarch central cylinder are not fused together. The cortical cells in these roots contain hyphæ which form balls in them.

Regarded anatomically there is a difference between the vertical and the horizontal part of the rhizome, in that the former has a phellogen which, according to Marié, develops from 3 or 4 outer layers of the cortex. The cork is 3—5 layers thick. The horizontal rhizome, on the other hand, retains its small-celled epidermis which has arching and fairly thick outer walls. The cortex is almost similar in both parts of the rhizome and is rather compactly built of cylindrical cells which, especially in the vertical part, are rich in starch. The starch-grains are either single or compound. In the horizontal part of the rhizome there is a continuous wood-ring; the

number of the bundles is indicated by the isolated groups of sieve-tissue. The cambium is no doubt always rudimentary. The endodermis which surrounds the central cylinder is fairly distinct. In the vertical part of the rhizome, on the other hand, the bundles are separated more or less from each other and leave room for the medullary rays, of which the elements are much elongated in a radial direction and are non-lignified. The cambium is capable of division but is fascicular only. In the outer part of the wood large vessels occur in fairly distinct, tangential layers separated by wood-parenchyma, an arrangement which recalls the formation of annual rings. The primary wood has smaller vessels than has the secondary. Secondary cortex is developed only to a slight extent. The pith cells are crowded with starch especially those in the vertical part of the rhizome.

The peduncle is somewhat furrowed; the epidermis consists of small cells, the outer wall, especially, is thick and is provided with a smooth cuticle. The stomata project somewhat (Fig. 58, *A*); the epidermal cells contain a small amount of chlorophyll. The cortex consists of 5—6 layers of fairly closely-placed, cylindrical cells with rather thick walls. The bundles number about seven and are closed and have on the outside a fibrous tissue, 3—4 layers thick. Upon the inner side of the wood from one to two layers of slightly developed wood-parenchyma occur; between the latter and the vessels, there is, in the larger bundles, some non-lignified parenchyma, and between the large group of sieve-tissue and the vessels some wood-parenchyma. An interfascicular, and in part fairly strong, mass of lignified-parenchyma, about four layers thick, is present; the pith is broken down in places in the fully developed axis.

Along the larger veins of the upper surface of the leaf there are a few small hairs. The outer walls of the epidermal cells of both the upper and the lower surface are fairly thick,

especially those of the upper; the radial walls are markedly undulating, and almost equally so upon both sides (Fig. 58, *C*, *D*). Upon the upper surface there are only a few stomata, upon the lower about 350 per sq. mm.: they are fairly evenly distri-

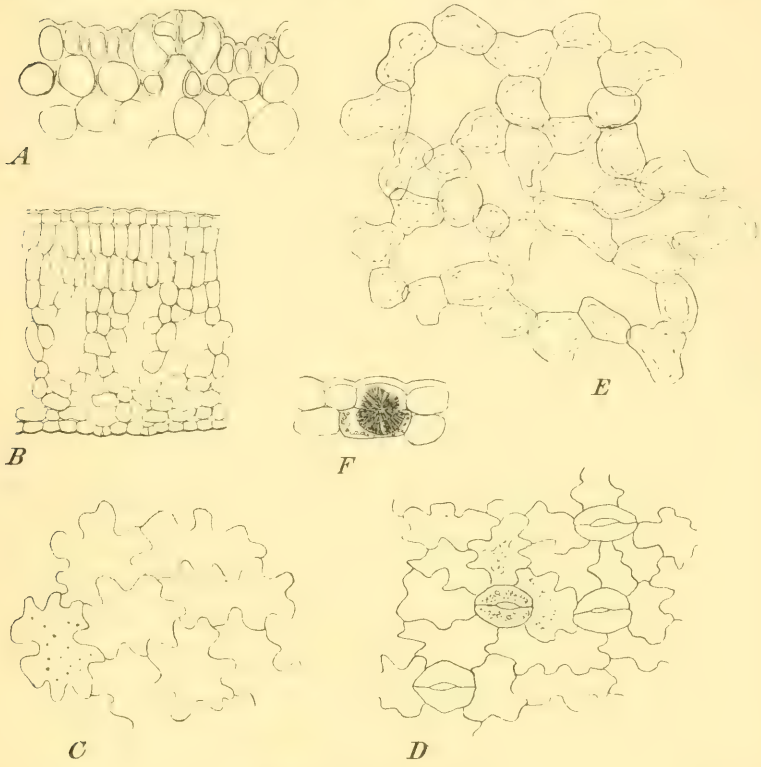

Fig. 58. *Coptis trifolia.*

A, Epidermis of the peduncle, showing a stoma (Godthaab; $^{300}/_{1}$). *B*, Transverse section of a one-year-old leaf (Godthaab; $^{130}/_{1}$). *C*, Epidermis of the upper surface of the leaf (Sukkertoppen; $^{300}/_{1}$). *D*, Epidermis of the lower surface of the leaf (Sukkertoppen; $^{00}/_{1}$). *E*, Section of spongy parenchyma, parallel to the surface, from a one-year-old leaf (Sukkertoppen; $^{300}/_{1}$). *F*, Sphæro-crystal from the cells of the lower surface ($^{300}/_{1}$).

buted, but are absent above the large veins. The direction of the stomata is almost similar to that of the principal vein of the leaf-lobe. The epidermis contains chlorophyll. In the young leaves the bundles are not accompanied by any especially well-marked stereom, but in the one-year-old leaves but-

tresses of strong stereom occur above and below the largest bundles; but in the case of the smaller bundles only below them; the smallest are entirely without stereom. There is in these leaves, upon the lower side of the sympodial marginal vein, an especially strong fibrous tissue extending to the epidermis, which is not the case with the other bundles.

The young partially expanded leaf is almost isobilateral in structure, and is without intercellular spaces of any size. Usually two palisade-layers are gradually differentiated and may constitute as much as one-half of the mesophyll, the cells occur close together and are about twice as long as they are thick. Large intercellular spaces are also gradually developed in the spongy parenchyma, and, as shown in the figure, are separated by vertical lamellæ. The transverse and the longitudinal sections are similar in this point.

No true epithema occurs, but the vein extends almost to the epidermis of the tooth of the leaf-apex, and upon the upper side of this tooth 2—3 stomata occur with the same appearance as that of the water-stomata in *R. nivalis*: stomata are absent from the under side of this tooth.

The leaves are rich in large, yellow sphæro-crystals (Fig. 58, *F*), especially abundant along the veins and under the epidermis; they are probably of substances which have been in solution in the living cell, but were precipitated by alcohol; their nature has not been more closely investigated.

The leaf-stalk, apart from its form, is similar in structure to the peduncle.

Summary.

I. The growth-form of the species which have been investigated may be referred to the following groups.

A. The *Primula*-type. The species referred to this group have a vertical, perennial rhizome, the primary root probably

dies early in all the species, and there is a well-marked principal bud in the uppermost leaf-axil of the rosette: *Ran. sulphureus*, *acer* and *affinis* which have only foliage-leaves, and *Ran. glacialis*, *nivalis* and *pygmæus* which have also scale-leaves.

To this group also *R. reptans* may be referred but the main axis is creeping. These species are *hemicryptophytes*[1].

B. *R. hyperboreus*, *lapponicus* and *Pallasii* belong to the same type: The adult plant has no rosette, the straight stem creeps above the ground or in the moss, and in *R. lapp.* and *Pallasii* the branches often grow obliquely downward. *R. hyperboreus* and *Pallasii* are without a well-marked principal bud. In *R. lapp.* a principal bud occurs. — *Hemicryptophytes*, or perhaps *R. lapp.* and *Pallasii* may also be cryptophytes.

Batrachium confervoides is no doubt nearest to this group; but is a *hydrophyte.*

C. *Anemone Richardsoni*, *Coptis trifolia* and *Thalictrum alpinum* may be referred to the same type: There is a creeping subterranean rhizome and a principal bud which occurs in the axil of the uppermost leaf in *Anemone Richardsoni* and *Coptis trifolia* and in the axil below the uppermost in the specimens of *Thalictrum alpinum* examined by me. There is no aërial stem. The rhizome of *Anemone Richardsoni* is monomorphic and bears foliage-leaves especially. *Coptis trifolia* and *Thalictrum alpinum* have a dimorphic rhizome, the horizontal part of which bears scale-leaves, while the vertical part with short internodes bears foliage-leaves and scale-leaves in regular alternation. In *Coptis trifolia* the leaves pass the winter in a green condition. — *Hemicryptophytes. Anemone Richardsoni* may perhaps also be a cryptophyte.

II. Flower-biology. The flowers in probably all the species are well-developed by the latter part of the summer

[1] Raunkiær: Planterigets Livsformer og deres Betydning for Geografien. København, 1907.

which precedes that in which they expand (cf. *R. pygmæus* and *nivalis*). All the species which have been investigated are entomophilous except the anemophilous *Thalictrum alpinum*; with the exception of that plant, they all have flowers which are fairly conspicuous, partly on account of their size being often rather large and partly on account of the colour of the nectary-leaves; these are yellow in the majority of the species but white in *R. glacialis*, *R. Pallasii*, *Batrachium confervoides* and *Coptis trifolia*. The perigone-leaves are green to yellowish-green.

The majority of the species are dichogamous although not to any great extent, and in all probability self-pollination usually takes place in cases in which cross-pollination does not occur. Again, the greater part of the dichogamous species is proterogynous with a homogamous stage at the end of the flowering period, viz. *Ranunculus affinis* (?), *R. sulphureus*, *R. nivalis*, *R. lapponicus* (also recorded to be homogamous), *R. Pallasii* (also homogamous), *Thalictrum alpinum* (also recorded to be homogamous) and *Coptis trifolia* which is proterogynous to some extent.

The protandrous species are *R. glacialis*, *R. acer* and *R. reptans*; also in these species the flowers ultimately become homogamous. In Denmark *R. acer* has, besides the hermaphrodite flowers, others that are diclinous.

R. pygmæus and R. *hyperboreus* are homogamous; the latter is recorded to be also slightly protandrous.

Some of the species are recorded to have fragrant flowers: *R. acer* (perfume slight), *R. sulphureus*, *R. nivalis* and especially *R. Pallasii* and *lapponicus*.

All the entomophilous species have nectaries except *Anemone Richardsoni*. In the majority of the species of *Ranunculus* the nectary is covered by a simple scale; in *R. acer* this is irregularly lobed at the free edge; in *R. glacialis* the nectary is naked, but a lobed scale is seated above it. In *Batrachium* the nectar-pit is naked.

Insect-visitors have frequently been observed in the species of *Ranunculus*, usually small Diptera.

III. Fruit-dispersal. The fruit is doubtless dispersed by the agency of the wind, but it appears that in some species synzoic dispersal may also occur (*R. glacialis*, *nivalis* and *acer*).

IV. The germination is known only in a few species; in some, it takes place during spring, in others during autumn. *R. glacialis* is remarkable by the fact of its having only one cotyledon.

V. The roots, in the specimens which have been investigated, fall naturally, according to their anatomy into three groups.

A. In all the species of *Ranunculus* and in *Batrachium confervoides* the primary structure is retained. The epidermis is thin-walled and has a tendency to collapse (except in *R. acer*); the exodermis is usually distinct, and the radial walls are undulating; both layers are suberized. In several species the two outermost layers of the cortex are slightly collenchymatously thickened; in this respect the species with creeping stems form an exception. The median part of the cortex is more or less broken down, often to a great extent; the degree of disintegration is probably dependent not only upon specific differences but also upon the lesser or greater degree of humidity of the locality. Around the usually thin-walled, suberized endodermis some layers of the cortex are always retained. *R. acer* has a thick-walled endodermis. The central cylinder is usually diarch to tetrach. The pericycle is one-layered; on the outside of each group of sieve-tissue there is more or less distinctly to be seen in all the species a large, pentagonal sieve-tube wedged in between adjacent cells of the pericycle.

The roots of the second order agree with the above description, only the exodermis is probably not suberized and none of the layers are collenchymatous.

The following species had endotrophic mycorrhizas,

which occurred almost exclusively in roots of the second order: *Ran. sulphureus*, *acer*, *affinis*, *nivalis* and *pygmæus*. Hesselman, in his paper "Om Mykorhizabildningar in ark. Växter" (Bih. Kgl. Sv. Vet. Akad. Handl. Bd. 26. Afd. III), mentions no *Ranunculaceæ*. — Root-hairs were found in *R. glacialis*.

B. The roots of *Anemone Richardsoni* and of *Coptis trifolia* are very similar. The epidermis is strong; the exodermis is not very prominent and the cell-walls of it and of the rest of the cortex are fairly thick; the intercellular spaces are very small; no broken-down parts were observed. The endodermis has somewhat thickened walls which were found to be suberized. The central cylinder of *Anemone Richardsoni* was found to consist altogether of primary elements; in *Coptis trifolia* some secondary wood is developed; from two to three radial masses of wood occur. In both species spongy hyphæ occurred in roots of the second order. — Roots-hairs were found in *Coptis trifolia*.

C. The roots of the first order in *Thalictrum alp.* have vigorous secondary growth in thickness; the primary cortex is thrown off. The outermost layers both in the latter and in the secondary cortex have collenchymatously thickened walls. The primary radial masses of wood number from three to six. The secondary roots are of primary structure and are peculiar owing to the presence of a dimorphic epidermis; they were found to contain spongy hyphæ.

VI. The vertical rhizome in the species of *Ranunculus* of the *Primula*-type is very similar in structure in the different species; usually it is schizostelous. In regard to *R. acer*, a smaller amount of lignified elements was observed in the specimens from the northern localities than in those investigated from Denmark.

VII. The stem and the peduncle in all the species, were found to be on the whole similar in structure. The bundles are closed and are arranged in a ring. The strength-

ening tissue occurs close to the bundles; it is almost entirely absent from certain species and is fairly well developed in others; it consists of two parts — the fibrous tissue outside the leptome, and a band of lignified parenchyma uniting the bundles. Both in the stem and in the rhizome of *R. acer* a smaller amount of stereom occurred in the specimens from the northern localities than in those from Denmark. The nodes in the species of *Ranunculus* with creeping stems resembled in structure the rhizomes in the species with *Primula*-structure.

In several cases the monostelic structure mentioned by Marié could be demonstrated in the peduncle while the rest of the stem was more or less distinctly schizostelous.

The pith was often found broken down.

The cortex was very loose in structure in the majority of the species (cf. for instance *R. glacialis* and *Pallasii*) and very often great parts of it were broken down. *Anemone Richardsoni* and especially *Coptis trifolia* and *Thalictrum alpinum* had a firmer cortex than had the other species, and the epidermis in the last two had also a more xerophytic character; in the species of *Ranunculus* it was rather thin-walled; the cuticle was usually found to be thin and striped. The epidermis contained chlorophyll in all the species, often in great quantities; the stomata were either on a level with the surface or projected slightly.

VIII. The structure of the leaves. The species which have been investigated may be referred to two large groups, viz., the submerged-leaved and the aërial-leaved.

A. The typical submerged leaves in *Batrachium confervoides* and *R. reptans* are cylindrical and more or less radial; *Batrachium* has one bundle in each lobe, *R. reptans* has no doubt usually three in each leaf. When these plants grow in dry localities the leaves of both species react in a similar manner and approach the bifacial type to which the elliptical leaves of *R. reptans* may be referred entirely. The submerged

leaves of these two species have no stomata and few stomata respectively; in the bifacial leaves they are more numerous upon the upper surface.

B. The aërial leaves. All the species of *Ranunculus* with the exception of *R. reptans* and *R. glacialis* may, with regard to the structure of their leaves, be referred to the same sub-group. The leaves are glabrous or slightly hairy (except in *R. acer*), the epidermis is thin-walled and the palisade-tissue and spongy parenchyma are homogeneously developed in all the species; from one to two palisade-layers occur which constitute about one-half of the thickness of the mesophyll, and the individual palisade-cells are often barrel-shaped and somewhat irregular; the spongy tissue contains numerous intercellular spaces and the cells are branched in a stellate manner. In *R. hyperboreus* the stomata were more numerous upon the upper surface, and in *R. Pallasii* their number was equal upon both surfaces, but in the other species they were more numerous upon the lower surface. The habitat of all is usually damp moss.

R. glacialis differs from the above-mentioned species in its better developed palisade-tissue and in the looser structure of its spongy parenchyma. The stomata are most numerous upon the upper surface. It grows in localities which are poorer in humus than those in which the other species of *Ranunculus* grow.

In Greenland *Anemone Richardsoni* is doubtless especially a shade-plant; in the structure of its leaf it closely resembles *Anemone nemorosa*. Stomata occur almost exclusively upon the lower surface of the leaf.

Of the species which have been examined *Thalictrum alp.* and *Coptis trifolia* are the most xerophytic. The leaves are coriaceous and the epidermis is thick, especially in *Thalictrum alp.* The palisade-cells occur in 2—3 compact layers; the spongy parenchyma consists of shortly branched cells. In both species

stomata are almost absent from the upper surface, but occur very numerously upon the lower surface. *Thalictrum alp.* grows in very different localities. The fact that the leaves pass the winter in a green condition may perhaps account for *Coptis trifolia* being xerophytic.

As a peculiar feature common to all the species may be mentioned the fact that the epidermis contains chlorophyll. As is well-known this is the case in temperate regions in plants growing in scanty light, for example, in many aquatic and woodland plants; which appears to suggest that the species in question have not been exposed to intense light—at any rate not constantly. For further particulars the reader is referred to Lidforss [1] who states that a great many North-European evergreens have chlorophyll in the epidermis, especially that of the lower surface of the leaf; the epidermis there is often separated from the mesophyll by means of large lacunæ and it will then, on account of the presence of the chlorophyll, be more independent in regard to its nutrition-physiology.

Of the 14 species which have been investigated the stomata, in the majority, were most numerous upon the lower surface, viz. in *R. affinis, acer, sulphureus, nivalis, pygmæus, lapponicus, Anemone Richardsoni, Thalictrum alp.* and *Coptis trifolia*, nine in all. Of these *Ran. lapponicus, Thalictrum alpinum* and *Coptis trifolia* have probably none, as a rule, upon the upper surface. *R. Pallasii* has an almost equal number upon both surfaces, a fact which perhaps is connected with the position of its leaf, the lamina continuing the direction of the stalk. The following species have the greater number upon the upper surface: *R. glacialis, hyperboreus* (its leaves are sometimes floating-leaves), *R. reptans* and perhaps *Batrachium confervoides*, the last two in their aërial leaves. Börgesen (l. c.) states that

[1] "Die wintergrüne Flora." Lunds Universitets Årsskrift, N. F. Bd. 2, Afd. 2, No. 13, 1907.

the majority of the species which he has examined had the stomata most numerous upon the upper surface.

All the species of *Ranunculus*, *Batrachium confervoides* and *Anemone Richardsoni* were furnished with hydathodes and epithemata at their leaf-apices. It is usual for the water-pores to occur marginally upon a somewhat upwardly-directed surface, and in all these species the epithema is essentially similar in structure; the tracheids are somewhat spreading and terminate at the intercellular spaces, and the cells of the mesophyll are shortly branched and have strongly undulating walls. Chlorophyll is usually absent from the epithema and the nuclei of the cells were remarkably large.

From the consideration of the above it will be seen that the species which have been investigated are very similar in regard to the greater part of their structure; and, as is natural, the similarity is especially conspicuous in the relatively numerous species of *Ranunculus*; it has also been shown that in the material at hand no considerable differences have been able to be demonstrated in the individuals of the same species from different regions (see however *R. acer* and *R. affinis*).

27—6—1911.

7.

Lentibulariaceae.

(Pinguicula).

By

Fr. Heide.

1912

INTRODUCTION.

This paper has, like the preceding ones of the same series, a two-fold purpose: the one to contribute to a better knowledge of the relation between the arctic plants and the conditions under which they live, and the other to serve as a basis for future studies of a similar nature.

I think I have contributed towards the first-mentioned by distinguishing two types in my material: an arctic and a temperate one and by confining my representation to this main point, and as regards the second I hope to have succeeded in some measure in pointing out the future way towards a closer treatment of the question. But on the whole my paper has, more and more, attained the character of a preliminary sketch, in which also the principles of my future works on this subject are laid open to criticism. The cause of this is, among other things, that on working up my subject I found that a material, collected several years ago, could not serve one and every purpose; the new principles for botanical treatment have outgrown the principles which determined the collection of the material, and the application of this has become more limited. In regard to ecological studies it will be necessary in the future to form new principles for investigations in Nature, as I have also had occasion to mention in the text.

The material for investigation I have received partly from the Botanical Museum in Copenhagen and partly from the "Riksmuseum" in Stockholm. The latter institution has very generously placed its perfect and beautiful herbarium at my disposal. The photographs have been taken by H. E. Petersen, Mag. Sc. The illustrations were drawn mainly by Professor Eug. Warming several years ago; on some points — all concerning morphology — I have naturally found it necessary to add new ones. The deter-

mination of the *Arthropodae*, caught by the arctic species of *Pinguicula*, has been kindly undertaken by Mr. K. L. Henriksen and W. Lundbeck, Mag. Sc., Inspector at the Zoological Museum in Copenhagen. For which I tender them my best thanks. Lastly, I wish to thank Mr. R. V. Hansen for his valuable aid in translating my manuscript.

The species mentioned in the following pages are: —

Pinguicula vulgaris ..... p. 447
Pinguicula alpina..... p. 469
Pinguicula villosa..... p. 470

With respect to the genus *Utricularia*, of which I have had an exceedingly scanty material for purposes of investigation, I can only confirm the facts already known.

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I. Morphology and Biology.

Pinguicula vulgaris L.

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NANDER. p. 353. FENNER. KNUTH, p. 305. SYLVÉN, 1905, p. 134; 1906, p. 75. SILÉN, p. 94. VELENOVSKY, pp. 338 og 972. OSTENFELD, p. 100.

Materials in alcohol from West-Greenland, Iceland, Norway.

Pinguicula vulgaris is nearly always confined to moist localities, though not to so great an extent as *P. villosa*. The localities are marshes with grass-covered surfaces and moist rocky walls; it is rarely found in Sphagnum. The plant grows most frequently on turfy soil, more or less mingled with sand, and on rocks with a thicker or thinner covering of earth, but it may also grow on loose detritus, and it has even been found in gravelly tracts (for instance together with *Azalea* and *Betula nana*); moreover it has been seen in places sometimes overflowed by the sea (NORMAN). According to the same author it is found up to 900 m. above sea-level.

It is a typical rosette-plant, perennial, and lives through the winter by means of a special hibernacle, consisting of small, solid scale-leaves, containing starch. The development from seed is as follows: The germinating plant (Fig. 1, *A*) begins with a distinct primary root, which decays however very early, and adventitious roots develop from the stem; there is but one cotyledon, furnished with stomata and more or less developed glands, probably unable to function as yet (Fig. 1, *B* & *D*). As regards morphological explanation of this cotyledon, a very eager discussion has been carried on from time to time, but so far, harmony on this point has not been attained. Concerning the different views expressed on this difficult question I refer the reader to: GAERTNER, 1791; BROWN, 1810; TREVIRANUS, 1838, 1839, 1848; ST. HILAIRE, 1838, 1841; WALPERS, 1848; KLOTSCH, 1848; WEBB, 1853; BUCHENAU, 1865; CASPARY, 1867; DICKSON, 1869; GOEBEL, 1891—93; MERZ, 1897; SYLVÉN, 1905; VELENOVSKI, 1907.

The young plant has long internodes until it reaches the light, which probably causes the formation of the rosette. When this stage is arrived at, the plant has a short rhizome, gradually

dying away at the hinder end, bearing the rosette leaves, and furnished with a few roots, an inch in length and somewhat constricted in their upper part. At first they are white and bear root-hairs, later on these decay, and the root is covered with a brown layer of cork. The size of the rosette-leaves

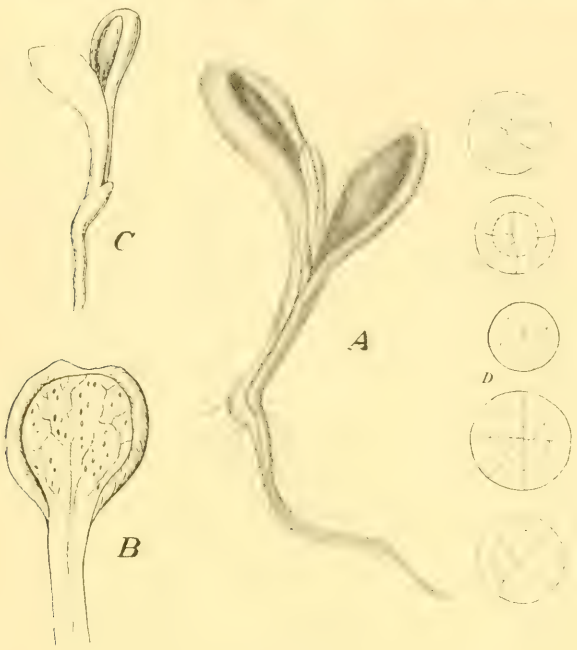


Fig. 1.

A, Seedling of *P. vulgaris* from the Færöes; this plant has been taken out from a colony of seedlings. *B*, Cotyledon of the same. *C*, Seedling of *P. alpina* from Tromsø. (E. W.; 1886) *D*, Different forms of glandular hairs from the cotyledon of *P. vulgaris*. (F. H.)

varies somewhat, but on an average seems to be a little smaller than that of those in our Danish specimens. With regard to the shoot-structure and the manner of growth some peculiarities are found in the arctic specimens of *Pinguicula*, which are not found in plants from more southern places. Therefore, I must mention the case a little more in detail.

The shoot-structure of *P. vulgaris* has been described very fully by Buchenau, later on Warming investigated the shoot-

structure of the arctic species and found that it agreed with Buchenau's description. The result of my investigations, however, does not show this. According to Buchenau the shoot-structure is the following: The plant, on reaching the light, develops its first rosette, the so-called "spring-rosette" which terminates in a flower: thus the main axis ends its growth. But at the time of flowering a rejuvenating shoot is seen in the axil of the uppermost foliage-leaf; this shoot develops into the second rosette "the autumn-rosette." While developing, it forces the fruit-stalk somewhat to one side, and often before the fruit is ripe, the stalk is flaccid and almost rotten. Simultaneously, the spring-rosette and its roots usually decay, and the autumn-rosette is now nourished exclusively by its adventitious roots. Towards the winter the leaves of the autumn-rosette decay entirely, and in the middle of the latter is now found the fully developed hibernacle which next year develops nto a new spring-rosette. In the case of the plant not flowering, both spring and autumn rosettes belong to the same axis.[1]

The description given here suits the shoot-structure of the "temperate" specimens of *P. vulgaris*, and in my material I have found the same to be the case in two specimens from Norway and the Færöes. That the same early decay of the fruit-stalk is found also in these plants I conclude from a peculiarity concerning the germination. I have received seedlings from Romsdalen (Norway) and the Færöes (Fig. 1, *A*), and

[1] Whether Buchenau is right in regarding the shoot-structure in *Pinguicula vulgaris* as sympodial I cannot decide at the present time. Professor C. Raunkiær has directed my attention towards the fact, that Irmisch regards the said shoot-structure as monopodial. This point naturally being of great interest I intend to investigate it more closely in the future, but in ecological respect and as regards my observations on temperate and arctic types of *P. vulgaris* the question has not any real importance, as will also be evident from the following representation. Whether the shoot-structure of *P. vulgaris* is sympodial or monopodial, the distinction between temperate and arctic types in the genus *Pinguicula* must be made nevertheless.

these are characterized by growing in small, compact tufts, resembling moss-tufts in form. The plants stand very close together and in considerable numbers in these colonies. The formation of these can only be explained by the fact, that the fruit-stalk has fallen down before the capsule had opened and that the seeds have germinated in a heap. So no real dispersal of the seeds has taken place in these two cases. Whether the colonies of seedlings mentioned here are common in temperate regions I myself have not been able to investigate, and in the literature of the subject I have never met with any notes regarding this fact.

Ecological studies on arctic plants should be based on species widely distributed both in cold and temperate regions, and then only can there be a possibility of an interesting comparison, and in this respect the genus *Pinguicula* is well qualified. It contains three species, inhabiting arctic and temperate countries, the one, *P. vulgaris,* thrives well both in the level lands of Central Europe and on rocky walls in arctic regions, another, an alpine species, and finally a purely arctic one, *P. villosa*. The most variable of these three, *P. vulgaris,* requires, however, everywhere in its wide geographical area, the same conditions, mainly with regard to water. The possibility of the arctic specimens being very differently formed in their anatomical characters from the temperate ones, must already in consequence of this be regarded as very small. On the other hand, the rather complicated shoot-structure of this species could better be thought to be subject to a reduction, produced by the conditions in arctic regions. Here, the late commencement of the summer will delay the development of the spring-rosette and, at the same time, of the flower (Hartz, Rosenvinge, Jónsson). The flowering, which takes place in Denmark usually in May—June, will for instance in Greenland not occur before June or July; in August—September the winter-bud must be developed because the night-frost comes already at this time. A reduc-

tion in the shoot-structure of *P. vulgaris* can thus be supposed, and what we find in this species as an adaptation to arctic conditions we likewise suppose will be found as a normal arrangement in the purely arctic species, *P. villosa*. My results will prove, that this supposition agrees with reality.

Already from a superficial investigation it must be remarkable, especially with Buchenau's results *in mente*, that the fruit-stalk with the wide-open capsule is always found in a stiff, erect position in the arctic specimens of *P. vulgaris*, collected in August (Fig. 5), sometimes also the fruit-stalk from the preceding year will be found. As already mentioned by Warming this is also the case with *P. villosa* (Fig. 14 A). From this it will first be seen, that the dispersal of the seeds is very complete in the arctic specimens of *P. vulgaris*. It is a well known fact, that the fruit-stalk of arctic plants is as a rule more inclined to remain in its place than that of plants of southern regions, and usually this circumstance is explained by the fact that the process of decay is exceedingly slow in the former regions. But this explanation does not settle the matter in regard to *Pinguicula*. Quite naturally the autumn-rosette requires space while developing, and the fruit-stalk must give way, at least it will be forced considerably away from its erect position. That this is never seen to occur in the arctic specimens of *P. vulgaris* must mainly be explained by the peculiarity that these never develop their autumn-rosette. In the material I have had for investigation I have succeeded in distinguishing two types of this species, a temperate one, agreeing wholly in its shoot-structure with Buchenau's description, and an arctic one, not previously recorded.

The latter develops as follows: In the spring the winter-bud produces a spring-rosette, the axis of which terminates in a flower; in the axil of the uppermost foliage-leaf is seen a rejuvenating bud, which does not develop into an autumn-rosette, but directly passes into its winter-rest as hibernacle (Fig. 2, A).

Whether a specimen belongs to the arctic or the temperate type, is not difficult to determine, provided the said specimen is collected in July or August, a time when the brown starch-filled scale-leaves of the winter-bud are fully developed. In the first case the leaves of the rosette surround the flower-stalk and

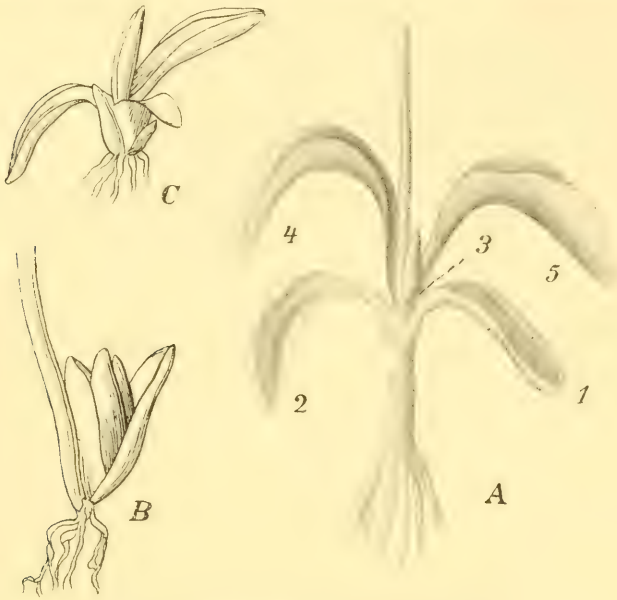


Fig. 2. *Pinguicula vulgaris*, arctic type.

A, Specimen from Kingua Kuanersok in Greenland, July 13; foliage-leaf No. 3 has been removed. (F. H.) *B*, Winterbud and fruit-stalk, Hammerfest, July 1. (E. W.) *C*, Winter-bud and half-developed spring-rosette, Kobbefjord, June 29. (E. W.); between the winter-bud and fruit-stalk foliage-leaves of the autumn-rosette are not developed. (Slightly magnified.)

the winter-bud, and the latter two stand close together without intervening rosette-leaves; this rosette therefore is a spring-rosette. But in the second case the leaves of the autumn-rosette are developed between the flower-stalk and the winter-bud, and then the latter is often forced away from its erect position. Besides, it is very easy to decide whether the rejuvenating shoot in the uppermost leaf-axil will develop into an autumn-rosette, or directly pass into its rest as hibernacle. In

the first case the rejuvenating shoot develops large, true foliage-leaves, placed in the axil of the uppermost leaf of the spring-rosette, but in the second case this at once develops thick brown scale-leaves, rich in starch (Fig. 2 *A*). This latter characteristic has the advantage, that it can be used in the determination of materials also from the early summer-time, naturally, with an exact result, only if spirit-materials are concerned.

The comprehension of the position of the winter-bud in relation to the flower-stalk and the character of the rejuvenating shoot are the key to the distinction between the arctic and the temperate type of the genus *Pinguicula*.

In the arctic type of *P. vulgaris* a reduction has thus occurred, though not a very strikingly deep one, but this reduction, however, indicates a peculiar adaptation to the shorter period of growth of the arctic regions.

Whether a similar reduction of the shoot-structure can be found in other arctic plants I have not been able to investigate, but *a priori* I should not think it impossible. The morphological type, here described as specially arctic, will be found again in *P. villosa*. The phenomenon which in *P. vulgaris* represents only an adaptation to the arctic climate, represents in *P. villosa* the normal shape. An autumn-rosette is never developed, but the rejuvenating bud directly passes into its rest as hibernacle (Fig. 3, *A* & *B*). One more peculiarity of the shoot-structure will further be found in *P. villosa*, but this is exclusively occasioned by certain circumstances of the soil in which it grows, and not by the influence of climatic factors; this case will not be mentioned more closely here.

P. alpina does not differ in shoot-structure from the ordinary temperate type; everywhere in its geographical area even in northern Scandinavia, it develops its autumn-rosette.

The fruit-stalk also in this species does not seem to be subject to quick decay; by the growth of the autumn-

rosette it is forced somewhat to one side (Fig. 4), but scarcely to such an extent as in the temperate type of *P. vulgaris*. probably occasioned by the circumstance that the leaves of the autumn-rosette are bent more slightly backward than are those of the spring-rosette. The tension, forcing the rosette-leaves close to the ground — a fact which will be treated later

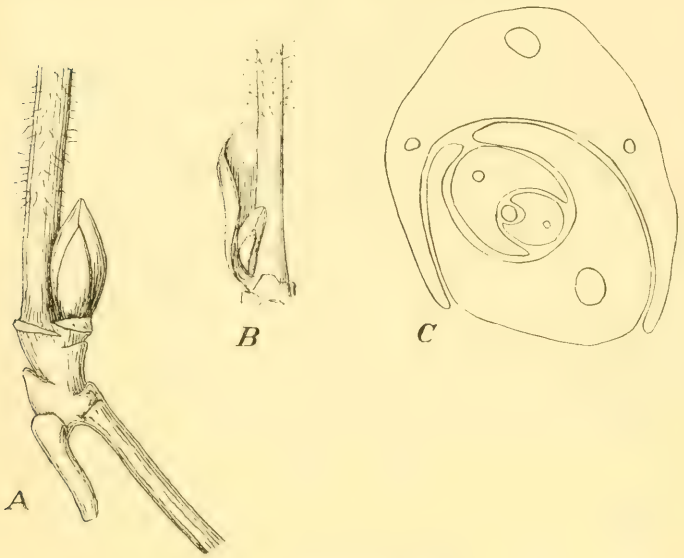


Fig. 3. *Pinguicula villosa.*

A. Winter-bud and fruit-stalk; the uppermost foliage-leaf has been removed. (F. H.) *B*, Winter-bud and fruit-stalk; the uppermost foliage-leaf is present. (E. W.) *C*, Transverse section of winter-bud. (F. H.) *A*—*C*, Vårstien. Kongsvold, Dovre (Norway; July), autumn-rosette is not developed.

on —, can scarcely be very strong in the autumn-rosette of *P. alpina*.

In connection with this distinction between the two types two questions must naturally arise. First, it would be interesting to investigate whether the short arctic period of growth has caused the said reduction to be a constant feature in these plants, and secondly we ought to endeavour to draw a limit for the southern extension of the arctic type of *P. vulgaris*.

Concerning the first of these points, however, I cannot for the present communicate any results, in the future I hope to be able to do so. *A priori* we may venture to think that *P. villosa*, if cultivated in Denmark, will continuously retain its arctic type, being undoubtedly, of the three species in question, the oldest inhabitant of arctic countries, and in herbarium material I never, even far down in Sweden, perceived any trace of development of an autumn-rosette. With respect to *P. alpina* there is nothing interesting to state on this point, but as regards *P. vulgaris*, the result of its cultivation is subject to greater doubt, and in consequence of this, such experiments with this species have a greater value. Whether the arctic type here is constant, it is quite impossible to say, though probability tends to the contrary.

Fig. 4.
Pinguicula alpina.
Autumn-rosette is developed; the fruit-stalk is pushed somewhat to one side by the rosette. Plateau de Murnau (Haute Bavière). June. About ½ natural size. (H.E.P. phot.)

Concerning the determination of a geographical limit, I have been more successful. *P. vulgaris* being a circumpolar species, one would with such a phyto-geographical line (a sort of Biochorus) be able to state the influence of the arctic climate upon a particular plant, and such a result would not be without interest. A line of this sort must naturally be exceedingly difficult to draw; in order to be able to arrive at a satisfactory result a great many observations in nature are required, made mainly in July or August. Only when this has been done in regard to the main points, will it be possible to proceed to the determination of the climatic factors distinguishing the two types.

If we take the opposite view and draw the geographical limit on the basis of the already existing climatological material.

one will attain more or less to the following result: The line will pass through the southern regions of British North-America, further to the east it will pass through Iceland and Western Norway, thereupon again with a southern direction through Sweden, Finland, Russia and Siberia. Further the height above sea-level will cause variations in the line in the different places.

Naturally I have not been able to draw this line even in

Fig. 5. *Pinguicula vulgaris*, arctic type.
Winter-buds and fruit-stalks. Autumn-rosette is not developed. Probably from the end of August. Ilua, Greenland. About $^2/_3$ natural size. (H. E. P. phot.)

a tolerably correct manner on the basis of the material at my disposal. For this the difficulties have been too great. In the first place the material has not always been collected in the season most suitable for my purpose; secondly, I have often been obliged to make my investigations on herbarium-plants in which the shoot-structure sometimes is very difficult to determine; last but not least, I have had from the greater part of the regions concerned only a few or no specimens at all for observation. If in spite of these great defects I have nevertheless decided to venture an experiment, I have done it especially because I think I may be able to give some sugges-

tions concerning the places, where future investigations on this point may be carried out with the greatest advantage. I naturally intend to investigate also this point in the future, but I am fully aware that it is impossible for me to do this thoroughly, unless others cooperate with me in the elucidation of the question.

I therefore communicate my results as quite premilinary:

Greenland.

In the fairly rich material from different places in West, East and South Greenland all the specimens seem to belong to the arctic type. (Dried and spirit material). (Fig. 2, *A* & Fig. 5.)

North America.

From this country I have had but two plants for investigation, therefore I cannot draw the line here. (1.) Labrador. specification wanting, arctic type. (2.) Quebec, Gaspé County, River St. Anne des Monts, August, temperate type. (Dried material.)

Iceland.

Eastern	Iceland.	Vallanes (Fig. 6).	arctic	type.
»	»	Seydisfjordur, July	»	»
Northern	»	Helgavatn. June.	»	» ?
»	»	Husavik. June.	»	» ?
»	»	Øfjord. Akureyri, June . . .	»	» ?
North-western	Iceland.	Dyrefjord, July.	temperate	»
Western	»	Reykjavik.	»	»
Southern	»	Westmanna-Islands, July. .	»	»
»	»	Hjørleifshøfdi, July	»	»
»	»	Ulfsvatn, Tvidægra, 500 m. above sea-level. July . .	arctic	»

This material is collected mainly in June or July, a season of the year, in which it is difficult to decide, whether an

autumn-rosette will develop or not in this locality, the value of this material is thus somewhat dubious (Dried material.)

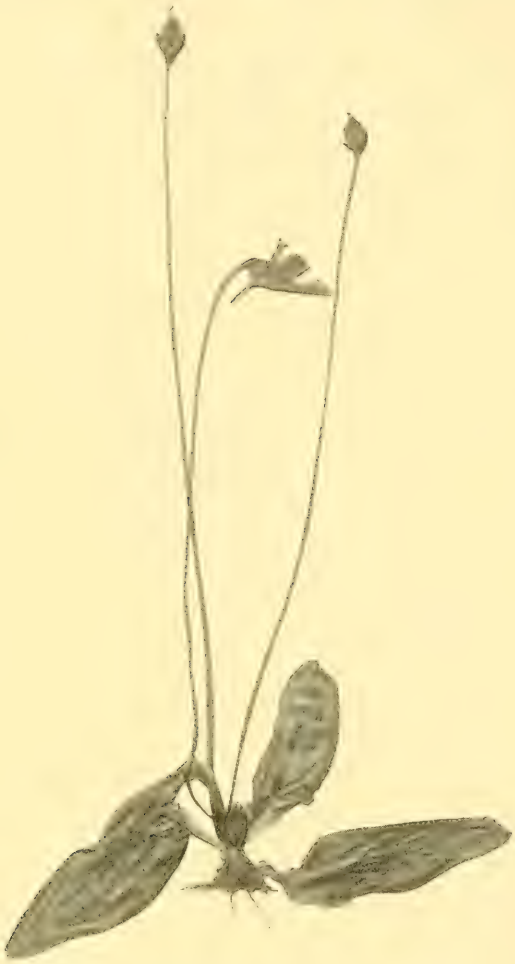


Fig. 6. *Pinguicula vulgaris*, arctic type.
Probably from August. Vallanes, East-Iceland (H. Jónsson).
About natural size. (H. E. P. phot.)

Norway.

File Fjæld, Nystuen, August . . . . . arctic type
Dovre, July . . . . . » »

Rørstad, Nordlandene, August . . . . . arctic type.
Tromsø, July. . . . . » »
Hammerfest, July (Fig. 2, *B*) . . . . . » »
Bosekop, July . . . . . » »

(Dried and spirit material.)

Fig. 7. *Pinguicula vulgaris.*

Vigorous specimens with long leaves and flower-stalks. Uppland. Upsala. Lassbybackar, June. About 1/3 natural size. (H. E. P. phot.)

Sweden.

Øland, Borgholm, July . . . . . temperate type.
Gotland, Visby, June . . . . . » »
Kinnekullen (Wenern), June . . . . . » »
Ornø (at Stockholm), June. . . . . » »
Stockholm, July . . . . . » »
Vermland, Gillberga, July . . . . . » »
Uppland, Sollentuna, Svartingeäng . . . . . » »
Medelpad, Njurunda, July . . . . . arctic »
» , Sundsvall, June. . . . . temperate »

Medelpad, Borgsjø, July . . . . . arctic type.
Jemtland, Storlien, July . . . . . temperate »
» , Åreskutan, August . . . . . arctic »
Lappmark, Quickjock, July. . . . . » »
» , Jukkasjärvi, July . . . . . » »
Luleå Lappmark, Karasjok, July. . . . . » »
» , Abisko, July . . . . . « »

Concerning the Swedish material, in Uppland there are circumstances, worthy of a closer investigation with respect to this point; whether a variation in the development of the autumn-rosette occurs here, I cannot say; regarded quite superficially it seems so (Fig. 7). Further the specimens from Øland and from the regions around Upsala are distinguished from the others by long, narrow leaves; long, distinct leaf-stems, and extremely long flower-stalks — in all plants grown under favourable circumstances; whether these forms, however, are produced by climatic or terrestrial influence, I am not able to decide (Fig. 8.). (Dried material.)

Finland and Russia.

Kajsana?, July . . . . . arctic type.
The peninsula of Kola (without further indication) » »
(Dried material)

According to these investigations Greenland exclusively presents the arctic type, the same is the case with the northern and eastern coasts of Iceland: the western and southern coasts of this island, on the other hand, present the temperate one. Probably, however, very complicated circumstances are found on this island, as already suggested by my synopsis. Probably the climatic circumstances, for instance in the inner parts of the fjords, will often cause the existence of the temperate type in the region, mainly inhabited by the arctic one, and in return the latter will be found in places in the region of the temperate one. No doubt the distance from the sea, both vertically and horizontally, will also cause great variations in the

course of the boundary line. Epecially from such geographical localities a large material is necessary to determine the influence of the arctic climate on the plant, and the material must, besides being of a botanical and meteorological nature, also contain more satisfactory indications as to the nature of the locality, than has hitherto been the case with the spirit-materials and herbarium-specimens in our museums. — From Iceland the line with probably go over the middle of the Scandinavian peninsula in a direction towards Sundsvall; an arctic deviation is found along Dovre and Filefjæld in Norway, and a corresponding temperate one along the west-coast of Norway; I am not able to say, how far to the north this is found. After this the line goes through Finland in a direction towards the south through Russia, Siberia and North-America. —

Fig. 8. *Pinguicula vulgaris.* Very vigorous specimen with long leaves and flower-stalks. Oland. Thorslunde. June. About 1/3 natural size. (H. E. P. phot.)

The shoot-structure in the genus *Pinguicula* evidently varies highly in the different species, found in different climates, and contains probably interesting deviations from the well-known case in *P. vulgaris.* An extensive comparison with respect to this point, will no doubt be valuable, but such a thing is naturally beyond the limits of this paper, I venture, however, in continuation of my treatment of the morphological peculiarities of the arctic species, to mention a single point concerning *P. caudata.* Taken together with

this species my temperate and arctic types show a fine phytogeographical scheme. Through a single period of growth the picture will be as follows:

I. Subtropical type. *P. caudata*. Mexico. Summer-rosette of the ordinary *Pinguicula*-type, terminating in a flower. The rejuvenating shoot in the axil of the uppermost foliage-leaf forms a winter-rosette like that of *Sempervivum* with short and thick leaves, filled with amylum and furnished with a large layer of cells filled with water. The glands are not fully developed. (Nourishment by insects is thus excluded in the winter-rosette). By this peculiar winter-rosette the plant passes the unfavourable season. Hibernacle is never developed. According to Sander also the winter-rosette can develop flowers. (Literature: Schlechtendal, 1832, p. 393. De Candolle, 1844, p. 28. Sander, 1881, p. 541. Hooker, 1882, pl. 6624. Godefroy-Lebeuf, 1883, p. 387. Duchartre, 1887, p. 207).

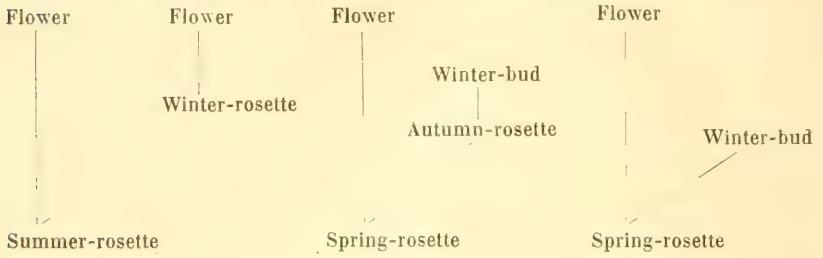
II. Temperate type. *P. alpina* and *P. vulgaris*. Spring-rosette, terminating in a flower. The rejuvenating shoot in the axil of the uppermost foliage-leaf develops an autumn-rosette, in the middle of which the winter-bud is to be found; both rosettes are of the ordinary *Pinguicula*-type.

III. Arctic type. *P. vulgaris* (arctic specimens) and *P. villosa*. Spring-rosette, terminating in a flower. The winter-bud is directly formed from the rejuvenating shoot in the axil of the uppermost foliage-leaf. Autumn-rosette does not develop.

The three types, here mentioned, show the main characters of the forms produced in different climates; between the two first I am not able to demonstrate a transition. But I see an evident transition between the two last types in *P. vulgaris*.

Also in the rare *P. vallisneriaefolia* there seem to be circumstances, worthy of closer investigation with regard to the shoot-structure. The literature, however, gives but few and uncertain indications on this interesting point. (Webb, 1853, p. 48. Buchenau, 1865, p. 62.)

Diagram of the shoot-structure in the genus *Pinguicula*.



I. Subtropical type. *P. caudata.*

II. Temperate type. *P. alpina* and *P. vulgaris.*

III. Arctic type. *P. vulgaris* and *P. villosa.*

As already mentioned there exists a peculiar tension in the leaves, causing these to be always bent backward in exhumed specimens. The advantage of this is, that the middle of the rosette, and with this the young leaves, will always be forced up over the surroundings. The substratum in which this species, *P. vulgaris*, grows, being almost exclusively solid (not growing as is the case with the *Sphagnum*), and the tension always very strong, the leaves will easily be able to perform their work to perfection. This is not the case with *P. villosa*, as the following with show.

As is well known, the leaves are adapted to catch insects. The edges are incurved; according to Klein's experiments this circumstance prevents the escape of small insects. These are forced up under the incurved edge and are digested there. In a separate chapter a synopsis of insects, caught by the arctic specimens will be given collectively with respect to all three species.

Vegetable propagation usually occurs in temperate regions, the uppermost leaves in the autumn-rosette supporting small, often stalked bulbs, which, during the next year, develop into independent plants. As regards their main characters these

bulbs are formed like the winter-bud, consisting of small, thick scale-leaves, characterized by a strong brown colour, probably due to their contents of tannin. Whether this kind of vegetative propagation is found at all in the arctic type of *P. vulgaris*, which never develops an autumn-rosette, I cannot say, I never observed anything in that direction, but probably this work is undertaken by the spring-rosette, in which case vegetative propagation is, however, very scanty. I have been led to this conclusion mainly by a parallel circumstance in *P. villosa*, which will be mentioned later on. It is possible, that this limitation of the vegetable propagation is balanced by the more regular dispersal of the seeds in the arctic species, but in order to be able to judge correctly on this point one must, however, also take note of the number of the seeds and their power of germination, which, for the time being, I have not been able to do.

Concerning the quantity of the flowers a statistic synopsis shows a difference between temperate and arctic types. In the former 3—4, and even 10 flowers are very commonly found on the same plant, while ordinarily only one flower occurs on the latter. In a single case I have observed traces of development of an inflorescense, the same, as will be mentioned in the following, has been observed in *P. villosa* (Fig. 16) and can perhaps give a hint regarding the true explanation of the inflorescense in the genus *Pinguicula*, a question which has however no interest in a communication regarding the special nature of the arctic plants. I only refer the reader to Buchenau's and Wydler's somewhat dubious explanations on this point.

With respect to the temperate type the biology of the flower has been investigated by many inquirers, the arctic one has been studied in the best and most detailed manner by Warming. My investigations can only confirm and, on a single point, supply Warming's results. As is well known,

the case is usually as follows in *P. vulgaris*: The flower is homogamous, and self-pollination is prevented by the foremost part of the stigma being very large and stretching far beyond the anthers so that these latter are totally covered. The hindmost part of the stigma is on the other hand small and sometimes divided into two (Fig. 9, *B*). The anthers open with a longitudinal slit closely below the stigma. The proboscis of

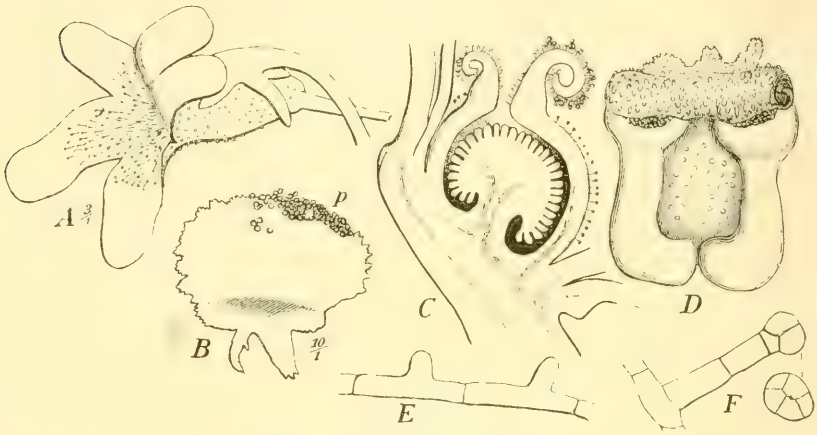


Fig. 9. *Pinguicula vulgaris.*

A, Flower; the entrance is not well-drawn; it ought to be somewhat wider. *B*, A stigma, the hindmost part of which has been divided into two lobes; p. pollen-grains. *C*, Longitudinal section through pistil; the foremost part of the stigma has rolled backwards down to the anthers. *D*, Pistil with the stigma, rolled backwards, and the two anthers, seen from front. *E*, Different forms of hairs from the spur (see also *H* in Fig. 10). *F*, A glandular hair from the inner wall of the spur; the head is seen also from above. (E. W.; 1886). *A*, From Tromsø; *B*—*F*, From Godhavn in Greenland.

the insect, when entering the flower, first touches the foremost part of the stigma, and when withdrawn this part of the stigma is bent aside, and the insect is furnished with pollen. After this the elastic stigma again springs back and covers the anthers. Owing to this circumstance self-pollination must be impossible, but in the arctic specimens the case is different. Warming has sometimes found the foremost part of the stigma rolled in such a manner, that its upper surface was brought into close contact with the pollen-masses (Fig. 9, D); this I have observed

in the majority of the arctic flowers in my material. Whether this peculiar phenomenon is caused by a natural tension in the stigma or by the agency of an insect I cannot decide, though its frequency makes the first mentioned explanation probable. In the cases mentioned here the stigma has been

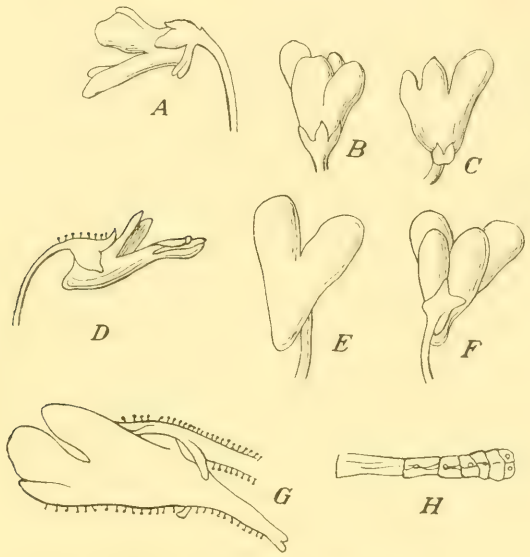


Fig. 10. *Pinguicula vulgaris.*

A—C, A flower, seen from different sides; it had two rudimentary anthers, but the pistil was normal. *D—F*, A flower with only one anther; the pistil was normal; *D*, Side-view; *E*, front-view; *F*, back-view. *G*, A flower with a spur, slightly divided into two parts. *H*, A hair from the inner side of the corolla. *A—F*, From Tromsø; *G—H*, From Godhavn in Greenland (E. W.)

thickly covered with germinating pollen (Fig. 9, *B*, *C*, *D*). According to all investigators only very few insects visit the flowers of *P. vulgaris*, and in the arctic countries, where larger insects are fewer in number than in other regions, the necessity of self-pollination must be exceedingly great. This agrees very well with the usual explanation of the biological circumstances in arctic countries: that self-pollination is, as first mentioned by Warming, very common here.

The hairs in the inner parts of the flower and their distribution has likewise been described in detail by Warming. I shall only mention the different types which occur: 1) Glandular hairs, but the glands are not sessile, as they are found to be on the foliage-leaves. Morphologically these hairs probably correspond with the long glandular hairs of the leaves (Fig. 9, *F*). 2) Fig. 10, *H*. These hairs are likewise multicellular; sometimes there is an indication of the development of a glandular head. 3) Short cylindrical papillæ, mere prolongations of the epidermis; these are found in the spur only (Fig. 9, *E*). The importance of these hairs is yet unknown, their secretum is mucilage, as far as investigated. According to Stadler their secretum serves as an alluring matter for insects, at any rate in *P. alpina*; this species being wanting in honey. It does not seem to be very wrong to use this explanation regarding all the hairs in the flower of *Pinguicula*. The flower is visited by small insects, which are however valueless to it, and are found dead in the spur. Among the small animals, found in the inner parts of the flower, Warming mentions a *Rotatoria*, a circumstance, taken by him, however, to be a mere casualty. In flowers from Denmark I have observed a great many indeterminable parts of chitin, as well as wings, parts of legs, small *Homopterae*, *Acarinae*, etc., together with some black, indeterminable masses of organic nature: in the arctic specimens I have found the latter only. The above-mentioned contents of the spur seem to support Stadler's views.

Further it must be mentioned, that deformations are often found in the flowers of the arctic specimens of *P. vulgaris*, some examples are figured in Fig. 10; whether the arctic type is different from the temperate one on this point I cannot say, but it does not seem to be probable. Other examples are mentioned by Rosenvinge (1896 a.)

In specimens from Denmark and the Færöes Rostrup has found an *Ustilago* (*U. Pinguiculae* Rostrup): this I have not observed in arctic specimens.

Pinguicula alpina L.

Doll, p. 383. Wydler, 1851, p. 420; 1857, p. 607. Hildebrand. Müller (1893) 1881, p. 352. Winter, p. 78. Klein, 1883, p. 163, tab. IX & X. Warming, p. 27. Stadler, p. 51. Loew, p. 53. Norman, p. 863. Sylvén, 1906.

Materials in alcohol from northern Scandinavia.

In arctic regions this species is found mainly in the same localities as *P. vulgaris* and often growing together with the latter; perhaps it goes a little higher above sea-level in Scandinavia, to about 1000 m (Norman). According to Klein it exists in two varieties, a yellow-green one and a more reddish one; to separate these in my Scandinavian material has been quite impossible. The shoot-structure has been mentioned under *P. vulgaris*. In a biological respect (Fig. 12) it behaves somewhat differently from *P. vulgaris*. The arrangement of the genitals however is the same as in the latter, but self-pollination is prevented by a slight protogyny. It is visited by flies, on the whole the visits of insects are much more frequent than in the two other species, both the yellow spots on the underlip and the wider entrance to the spur and to the genitals serve as honey-guides. According to Müller it is a "Fliegen-Klemfallenblume." Honey is absent, but its part is performed by the mucilage, secreted by the glandular hairs in the inner part of the flower (Stadler).

Fig. 11. *Pinguicula alpina*. Richly flowering specimen. Plateau de Murnau (Haute-Baviére). May. About 3/4 natural size. (H. E. P. phot.)

In *P. alpina* Winter found an *Ustilago*; this I have not observed in any Scandinavian specimen.

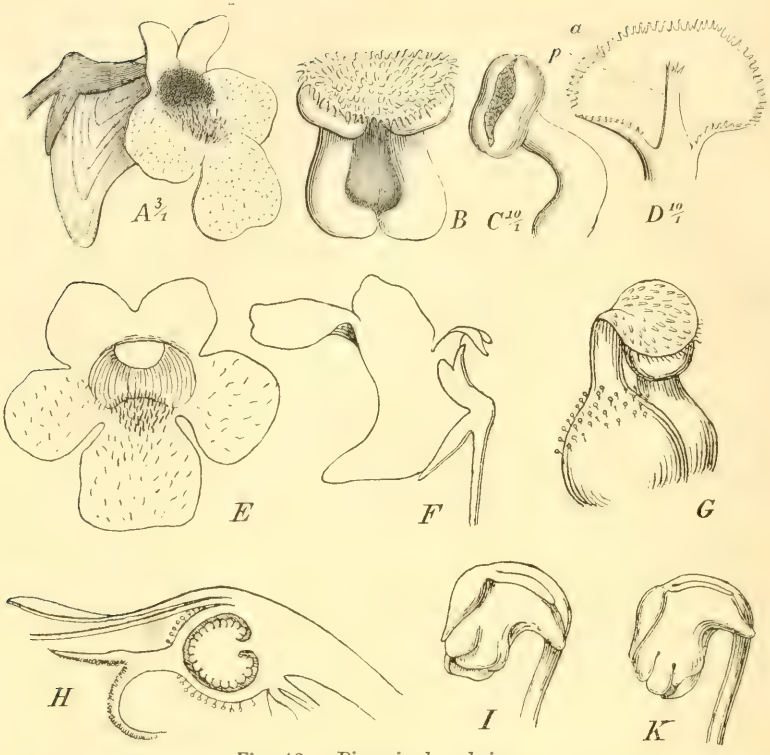


Fig. 12. *Pinguicula alpina.*

A, Flower; the entrance is drawn not wide enough (cf. *E*). *B*. The pistil and the anthers are almost covered by the stigma. *C*, An anther in act of dehiscence. *D*, The stigma, back-view. *E*, A flower, front-view (7/2). *F*, The same, side-view (5/2). *G*, The pistil and the one anther; the foremost anther has been removed (10/1). *H*, Longitudinal section through pistil (10/1). *I* and *K*, Rudimentary flowers; the anthers were open, the pollen-grains were filled with amylum (3/1). All the specimens are from Tromsø (Norway), June 28. (E. W.)

Pinguicula villosa L.

Wichura, p. 419. Axell, p. 44. Lange, 1880, p. 72. Warming, p. 27. Goebel, p. 116. Loew, pp. 89 og 116. Norman, p. 867. Sernander, p. 351. Sylvén, 1906.

Materials in alcohol from northern Scandinavia.

This species is in a higher degree than the two preceeding ones confined to moist localities, its habitat always being the water-filled substratum of the *Sphagnum*-cover. The rosette has but a few leaves, usually only two or three leaves are able to

function, on the whole the plant is smaller and weaker than the two other species (Fig. 14, *A*). The main characters of its shoot-structure have already been mentioned under *P. vulgaris*, it only remains to mention a circumstance pertaining to its manner of growth, caused by the more or less rapid growth of the *Sphagnum*. As the plant is always struggling with this factor, it is compelled to develop shoots with more elongated internodes than is *P. vulgaris*, which grows on a more solid substratum.

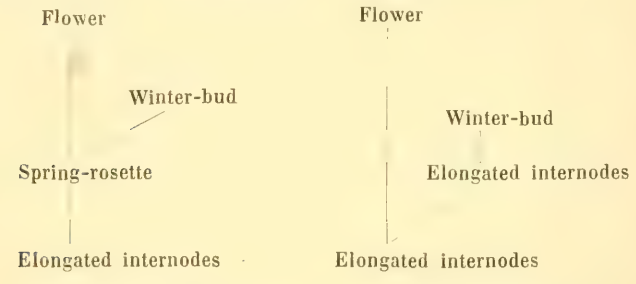
Fig. 13. *Pinguicula villosa.* A plant, which in spring did not reach above the Sphagnum, and therefore has not developed its spring-rosette; the rejuvenating shoot has formed elongated internodes instead of forming a winter-bud. Not before the shoot reaches to a suitable depth below the Sphagnum-surface, will the winter-bud develop. The plant belongs to those which are unfitted for the struggle for existence. Lulea Lappmark, Quickjock, July. About 1½ nat. size (F. H.)

In spring the plant grows with elongated internodes, until it gets above the *Sphagnum* and reaches the light, when it develops its rosette. The tension in the leaves of this species being undoubtedly very weak, the plant must be forced upwards during the summer almost exclusively by the *Sphagnum* pressing on its stem and leaves, until the the winter-bud develops and the foliage-leaves decay totally; then the *Sphagnum* grows forth and covers the plant for the winter. The manner of growth is here quite similar to what is known from *Drosera* (cf. Th. Nitschke: Wachsthumsverhältnissen d. rundblättrigen Sonnenthaues. Bot. Zeit, 1860, p. 57). Only when the plant does not at first reach above the *Sphagnum* during its growth by elongated internodes is the case then somewhat different (Fig. 13). The plant will then develop flowers without having formed a spring-rosette, and the rejuvenating shoot will develop with elongated internodes, instead of forming a winter-bud at once. Later on, when the growth of the *Sphagnum* diminishes, the rejuvenating shoot develops a winter-bud at its apex, at a proper distance from the surface of the *Sphagnum*. By this

arrangement it gains a possibility of reaching above the *Sphagnum* in the following year. That the phenomenon is not, as I at first supposed, caused by the influence of climatic factors on the plant, will be evident by the fact that it has only been observed in a very few specimens in all the collections from different places in Scandinavia, and to draw a geographical line between the two types, as I have tried to do from the mentioned supposition, and as I have done with *P. vulgaris*, is quite impossible here.

These specimens I can only regard as those which are unfitted for the struggle for existence, and this agrees very well with the fact that they are found mingled with the others, both in arctic and temperate regions.

Diagram of the manner of growth of *P. villosa*.



I. *P. villosa*, normal manner of growth.

II. *P. villosa*, constantly overgrown by the *Sphagnum*.

The leaves are very concave, often the edges are bent so closely together that the leaf is formed like a channel (Fig. 9, *A*). — As to vegetative propagation, I have, in spite of the rich material at my disposal, only observed it a very few times; from the lower parts of the rhizome, probably from the spring-rosette of the preceding year, a few shoots with elongated internodes had developed. But, as a whole, vegetative propagation is very scanty. Concerning the number of flowers, I

never saw more than one flower in the same period of growth. The biology has been treated by Warming; also as regards this species I can but confirm the facts already known. *P. villosa* is distinguishable in some main characteristics from the other

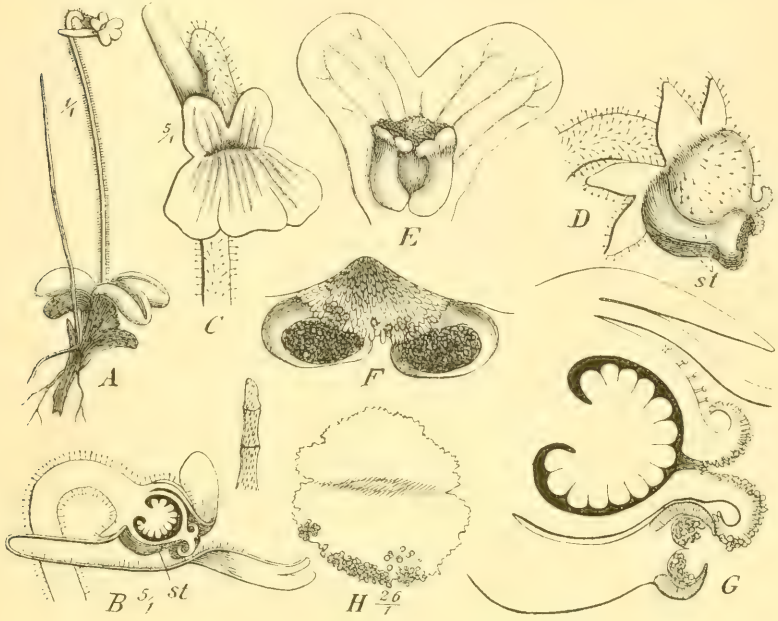


Fig. 14. *Pinguicula villosa.*

A, A plant (nat. size). *B*, Longitudinal section through flower; *st*, an anther. *C*, A flower, front view; the hairs of the lower lip are omitted. *D*, Pistil and anthers (*st*); the corolla has been removed. *E*, The upper lip with the pistil and the anthers. *F*, Within the upper lip the foremost part of the stigma and the anthers are seen from above. *G*, Longitudinal section, somewhat oblique, through a flower; the one anther is shown in section; the fibrous layer is indicated; the greater part of the pollen-grains has fallen out; the foremost part of the stigma has rolled backwards down to the anthers. *H*, The stigma, seen from above; the downward lobe is the foremost one. *I*, A hair from the middle part of the lower lip. Bosekop, July. (E. W.: 1886).

two species. The hindmost part of the stigma is always well developed, usually, however, it is smaller than the foremost one (Fig. 14, *H*.) According to Warming this fact proves that *P. villosa* represents a more primary type than the other two. Both parts of the stigma are furnished with papillæ on their upper side and are more or less bent backward (Fig. 14, *G*).

The foremost one is relatively much larger than that of *P. vulgaris* and *P. alpina*, and does not, as is the case with these species, cover the anthers (Fig. 14, *F—G*). The isolated upper lip with the genitals seen from the front shows the whole of the anthers,

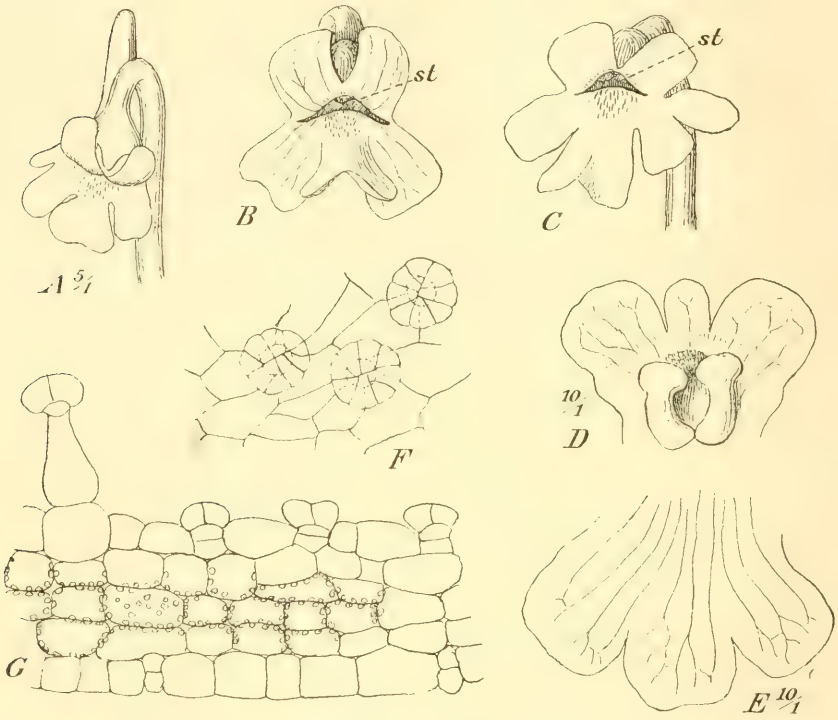


Fig. 15. *Pinguicula villosa.*

A—E, Different examples of deformed flowers; *st*, the anthers. *F*, Glandular hairs from the upper side of the foliage-leaf. *G*, Transverse section of a foliage-leaf. Bosekop (Norway). July. (E. W.)

and above them the stigma (Fig. 14, *F*). It has been proved that the subsidence of the foremost part of the stigma into the pollen results in the germination of the pollen-grains deposited thereon. On the whole, the pollen germinates very readily. Warming mentions his having found it germinating in different parts of the flower, and my investigations prove

Fig. 16. *Pinguicula villosa.*
Two specimens with an indication of inflorescence. Luleå Lappmark, Quickjock, Snjärrak, July. About 3/4 natural size. (H. E. P. phot.)

the same. Self-pollination seems thus to be a normal arrangement in *P. villosa.*

The hairs in the inner parts of the flower are as regards shape like those in the two other species, but as regards distribution and number they seem to be a little more scanty. As the figures show, deformations in the inflorescence as well as in the flower are found in this species (Fig. 15—16).

Summary. Finally in order to sum up in a few words the characters — both morphological and biological — which distinguish the arctic type of *Pinguicula* from the temperate one, the scheme should be as follows:

1. Reduction of the rejuvenating shoot.
2. Limitation of vegetative propagation.
3. Narrower and shorter leaves.
4. A smaller number of flowers.

5. A shorter inflorescence.

6. A greater possibility of self-pollination.

The ordinary type contains *P. alpina* and the temperate type of *P. vulgaris*, the arctic one, on the other hand, contains *P. villosa* and the polar-type of *P. vulgaris*.

As already mentioned, experimental culture alone will be able to prove whether the arctic characters are constant in the plants in question. Hypothetically, I have suggested that this will be found in *P. villosa*. In case such experiments give positive results in regard to the main points as regards *P. vulgaris*, we should be justified in classifying the arctic type, here mentioned, as a special variety, named *P. vulgaris*, *var. arctica*, but scarcely before this occurs.

Postscript to the chapter on Morphology and Biology. Since writing the previous chapter I have become acquainted with the following description by Alice Eastwood in "A descriptive List of the Plants collected by Dr. F. E. Blaisdell at Nome City, Alaska" (Botanical Gazette vol. XXXIII, 1902, p. 293):

"*Pinguicula arctica*, n. sp. — Leaves rosulate, glabrous, apparently fleshy, broadly ovate, sessile, obtuse, 1—2 cm. long, 5—8 mm. wide; scape purple, glabrous below, glandular-pubescent above, 1-flowered, 7 cm. high; calyx 2-lipped; upper lip of 3 deltoid divisions half as long as the lip, the sinus acute; lower lip narrower, with 3 shorter teeth and obtuse sinus one-third as long as the division; corolla purple, 11 mm. long, hairy within, with club-shaped hairs that extend to the lobes of the upper lip; lobes 3, orbicular, 4 mm. across; lower lip of 2 similar but shorter lobes; spur slender, tapering, 7 mm. long; stamens 2, with filaments dilated at base, nearly 2 mm. long, surmounted by capitate anthers; ovary orbicular, glabrous; stigma of 2 white broad plates, thin in texture.

This appears to be near *P. vulgaris*, but the corolla is of different shape and hairy within, while the spur is longer."

I cannot conclude my report on the morphology and biology of the two types of *Pinguicula* mentioned in this paper, without taking a stand as regards *P. arctica* A. Eastwood. It appears to me that the eagerness for finding new species, which is growing so rapidly in our days, may without injury to the future development of Botany be restricted considerably — at any rate we may be justified in demanding that it shall be kept within the limits of common sense. The features, in which *P. arctica* is said to distinguish itself from *P. vulgaris*, namely the shape and hairiness of the corolla and the length of the spur, are so uncertain and variable, that no careful investigator ventures to use these as a basis for the creation of a new species. The above-mentioned author does not know any of the features, which I have found peculiar to the arctic specimens of *P. vulgaris*, and in which they agree with the purely arctic species, *P. villosa*. I cannot believe that it will be possible to disregard these features totally, when a new arctic species of *Pinguicula* is to be created. Although "P. arctica" is our ultimate object, this has not yet been attained — either by Alice Eastwood or by any other investigator.

II. Physiology.

Linnæus, p. 10. Withering, p. 18. Darwin, p. 279. Morren, 1876 a; 1876 b. Pfeffer. Tischutkin, 1889, p. 346; 1891, p. 33. Goebel, p. 181. Fenner.

At first, as is well known, the genus *Pinguicula* was placed by Ch. Darwin in 1875 among the so-called insectivorous plants. Already long before this time the mucilagenous secretum of the leaves had been observed; further, it was known, that the secretum was able to cause the coagulation in milk (Linné,

Withering), and the plant has moreover been used medicinally. Buchenau supposes that the glandular hairs found on the leaves of the autumn-rosette, and especially the long, non-glandular hairs of the leaf-stems, serve to protect the winter-bud against the attacks of insects. Ch. Darwin was the first to make experiments here, and later on, his eminent works on this subject were followed by those of several other authors. Among these I must content to refer the reader to Goebel's on *P. vulgaris*, Klein's on *P. alpina*, and Warming's short remarks on *P. villosa*. Differing from the others are Tschutkin's works on the micro-organisms contributing to the process of digestion in *Pinguicula*, and though his views have already been strongly disputed, there would be some reason for making experiments of digestion in the arctic countries, where the activity of the micro-organisms is known before-hand to be very small. On the whole all earlier investigators of arctic plants have strangely enough passed by in silence the question of studying the processes of life in the arctic regions; that physiological experiments in themselves will not alone contribute highly to the knowledge of the economy of the arctic plants, but should also be the basis, on which the anatomical structure of the plants in question should be studied, I shall consider in a following chapter. Experiments on assimilation, respiration, transpiration etc., together with several quantitative analyses of the different parts of the plant certainly demand other abilities than those hitherto employed in the arctic botanical investigation, but seen from a merely historical point of view it is undubitable that the study of the ecology of the arctic plants will ultimate in an unnecessary period of dormancy, if the interest for this science does not create a new basis for it on physiological experiments.

With regard to the insectivorous plants the question on the importance of the digestion of insects, and the relation between the latter and the other physiological processes will

Synopsis of *Arthropoda*, caught by the arctic species of *Pinguicula*.

Species	Locality	Diptera	Homoptera	Thysanura	Araneïna	Acarina
P. vulgaris	Greenland (Kingua-Kuanersok) July, 1895	Chironomus sp. Sciara sp.		Achorutes sp. A. humicola Isotoma sp.		Erythræus sp. E. phalangioides var. gracilipes. Oribata sp. Bdella sp. Notaspis sp. Trombidium sp. Leiosoma sp. Nothrus sp.
P. vulgaris	Greenland (Ekaluit, Ameralik) July, 1895	Chironomus sp. Phytomyza?		Achorutes sp. Isotoma sp. Lipura sp.		Erythræus phalangioides var. gracilipes. Oribata sp. Bdella sp. Notaspis sp. Trombidium sp. Scutovertex sp.?
P. vulgaris	Greenland (Kingua Arpiksuit) July, 1890	Chironomus sp.		Achorutes sp. Lipura sp.	Thanatis sp? Theridium sp.	Oribata sp. Hypoaspis sp.?
P. vulgaris	Norway (Tromsø) 1885	Mycetophilus sp.?	Deltocephalus lividella (Larva)	Isotoma sp. I. viridis		Erythræus sp. Erythræus phalangioides var. gracilipes. Trombidium sp.?
P. alpina	Norway (Tromsø) July, 1883			Isotoma sp.? I. viridis		
P. villosa	Norway (Bosekop) 1885			Achorutes humicola. Isotoma viridis.		
P. villosa	Norway (Vårstien, Kongsvold Dovre) July, 1878	Chironomus sp.		Achorutes sp. Isotoma sp. I. viridis Lipura sp. Lepidocyrtus sp.		Trombidium sp.

further arise; but here we still want the necessary preliminary works from the temperate regions; the investigations hitherto made to clear up the most important question regarding the knowledge of the insectivorous plants cannot be used as a basis for arctic ecological studies. (Kellermann & v. Raumer, F. Darwin, M. Büsgen, etc.) —

A synopsis of the animals which serve as nourishment for the insectivorous plants in the different regions will perhaps be not quite without interest in the judgement of their economy; as far as I know, there has not previously been published anything save scattered and unsatisfying remarks on this point (Ch. Darwin, O. Penzig, Klinggraeff, etc.) The following synopsis is the first essay in the said direction, but naturally it is too defective to be able to afford a basis for any kind of judgement.

III. Anatomy.

Pinguicula vulgaris L. and Pinguicula alpina L.

Klein, 1880, p. 1401; 1882, p. 60; 1883, p. 167, tab. IX & X. Russow, p. 417. Van Tieghem & Douliot, p. 279. Dangeard & Barbé, 1887, p. 307. Dangeard, 1888, p. 260. Hovelacque, 1888 a, p. 262; 1888 b, pp. 641 & 713. Fenner.

The merely descriptive part of the anatomy of *P. vulgaris* has been treated so fully as regards the temperate type, that new facts can scarcely be added, and the differences between this and the arctic one seems so small, that, from a mere anatomical investigation, they appear to be alike. Also *P. alpina* and *P. villosa* (Fig. 15, *G*) do not present features which at the present time can be connected with the conditions in the arctic countries. But from this we do not venture to conclude that in the economy of the plants there are not found circumstances caused by the influence of climatical factors, and that the

arctic specimens in their anatomical structure are wholly like the temperate ones. The reduction in the rejuvenating shoot, mentioned in the first chapter, makes it precarious to us to stop at such an explanation. The plant being able to adapt its shoot-structure to a short arctic period of growth, it will be unreasonable to allow that no other elements in its organisation were marked by special arctic characters. When the merely anatomical investigation is not capable of giving a direct answer to this question, it will be the most natural way to make physiological experiments and use them as a basis for the judgement of the anatomical characters.

"Numbers are the metrical feet of science" says RAUNKIÆR, and it can hardly be doubted that the ecological studies will profit by a closer co-operation between physiology and anatomy, especially as these two sciences are not at present foreign to one another. When using in ecology exact physiological experiments as a basis, we are led to a wider view on the anatomical structure and to a greater continuity between the single facts of the latter, while it must be regarded as also quite settled, that such experiments will direct attention to several small features, to which no special value has hitherto been ascribed or which have been quite overlooked.

When I thus refrain from giving details as to the anatomical structure in the arctic species of *Pinguicula*, it is owing to the reason that for the present I can only state that they in every way agree with the temperate ones, and this I think is not in harmony with the facts; the fault is to be found, in this case, in the method, hitherto used, and the time for giving a minute judgement of adaptation to the conditions in the inner structure of these plants cannot arrive, before it can be made on a substructure of physiological experiments, performed in the regions, where the said plants are indigenous.

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